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Seasonal occurrence and parasitism of lepidopterous pests of crucifers, and host age selection by a potential control agent: *Trichogramma*.

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements of the degree of Master's in Sciences

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Abstract

M. Sc. Claude Godin Entomology

During a two years study (1993-1994) in southwestern Quebec, *Artogeia rapae* (L.) (Pieridae) and *Plutella xylostella* (L.) (Plutellidae) were found to be the most important lepidopterous pests of cruciferous crops (cabbage, broccoli, Brussels sprouts), followed by *Trichoplusia ni* (Hübner) (Noctuidae) and four minor species. The relationship between plant sampling and the use of degree-days, pheromone traps (*P. xylostella*) or butterflies counts (*A. rapae*) was assessed for *A. rapae* and *P. xylostella*. Three generations of *A. rapae* were observed annually, with a duration of 319.7 degree-days above 10°C (DD_{10}), while *P. xylostella* had three to four generations with a duration of 277.7 DD_{10}. Monitoring adults of both species may help to determine their periods of activity, but captures of *P. xylostella* were not linked to the level of infestations. By the end of summer, *A. rapae* was the most abundant species, especially on broccoli, while *P. xylostella* was often abundant early in the season. The complex of lepidopterous pests natural enemies was identified, and the data were analyzed using an illustrated parasitoid web. Fourteen parasitoid and three hyperparasitoid species (12 Hymenoptera, 2 Diptera) were identified. The most important parasitoid, *Cotesia rubecula* (Marshall), is a larval parasitoid of *A. rapae* that is newly established in Quebec. Overall, parasitism of lepidopterous eggs is almost not existent, whereas parasitism and infection of larvae and pupae by pathogens are important, but not significant to reduce butterfly populations. In order to evaluate the potential of oophagous parasitoids, the parasitism of up to 42 species/strains of *Trichogramma* was studied with different development stages of *P. xylostella*, *A. rapae* and *T. ni* eggs. Generally, *Trichogramma* females attacked preferably young eggs of a given host species. Females modified the number of offspring according to host size and host age, as fewer offspring emerged from the smallest or the oldest hosts. However, host age had no impact on sex allocation as expressed by offspring sex ratios.

Résumé

M. Sc. Claude Godin Entomologie

Au cours d'une étude de deux ans (1993-1994) dans le sud-ouest du Québec, les espèces de lépidoptères associées aux crucifères (chou, brocoli, choux de Bruxelles) identifiées comme les plus importantes ont été *Artogeia rapae* (L.) (Pieridae) et *Plutella xylostella* (L.) (Plutellidae), suivies par *Trichoplusia ni* (Hübner) (Noctuidae) et quatre espèces mineures. La relation entre l'échantillonnage des plants, l'utilisation des degrés-jour ainsi que de pièges à phéromones (*P. xylostella*) ou de décomptes des papillons en vol (*A. rapae*), a été déterminée pour *A. rapae* et *P. xylostella*. Trois générations ont été observées annuellement pour *A. rapae*, d'une durée de 319.7 degrés-jours base 10°C (DJ_{10}), alors que *P. xylostella* compte trois à quatre générations d'une durée de 277.7 DJ_{10}. Le suivi des adultes des deux espèces peut aider à connaître leurs périodes d'activité, mais les captures de *P. xylostella* ne sont pas reliées à l'intensité des infestations. *A. rapae* est l'espèce la plus abondante à la fin de l'été, surtout sur le brocoli, alors que *P. xylostella* peut être abondante dès le début de l'été. Le complexe d'ennemis naturels (parasitoïdes) des lépidoptères a été identifié et la trame reliant les différents niveaux trophiques a été illustrée. Quatorze parasitoïdes et trois hyperparasitoïdes (12 Hyménoptères, 2 Diptères) ont été recencés. Le parasitoïde le plus fréquent, *Cotesia rubecula* (Marsh.), est nouvellement établi au Québec et s'attaque aux larves de *A. rapae*. Pour l'ensemble des espèces de parasitoïde, le parasitisme des lépidoptères est presqu'inexistant au niveau des oeufs, alors que le parasitisme et l'infection des larves et des pupes par des agents pathogènes sont importants, mais leur impact est insuffisant pour réduire les populations à un niveau acceptable. Afin d'évaluer le potentiel des parasitoïdes oophages, la ponte de jusqu'à 42 espèces/souches de *Trichogramma* a été étudiée avec des oeufs de *P. xylostella*, *A. rapae* et *T. ni*, à différents stades de développement. En général, les femelles *Trichogramma* ont préféré s'attaquer aux oeufs les plus jeunes d'une espèce donnée. De plus, la taille de la portée a été modifiée pour tenir compte de la taille et de l'âge de l'hôte, les plus petites portées étant allouées dans les hôtes les plus petits ou plus vieux. Par contre, le rapport des sexes de la progéniture n'a pas été affecté par l'âge de l'hôte.

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I. INTRODUCTION

Cruciferous crops production in Quebec (cabbage, broccoli, cauliflower, Brussels sprouts) covers an area of 4 120 ha, for an estimated value of 32 million dollars in 1994, which represents 33% of the canadian production (Statistique Canada 1996). Among the numerous phytophagous insects associated with these crops, three lepidopterous species are of major concern to growers: the diamondback moth (DBM), *Plutella xylostella* (L.) (Plutellidae); the imported cabbageworm (ICW), *Artogeia rapae* (L.) (Pieridae); and the cabbage looper (CL), *Trichoplusia ni* (Hübner) (Noctuidae). The indigenous CL is polyphagous, whereas the other two species, accidentally introduced more than a century ago, are mostly restricted to members of the Crucifera family (Soo Hoo et al. 1984; Huang & Renwick 1993; Talekar & Shelton 1993).

These lepidopterous pests feed on foliage and bore into the commercially valuable parts of the plants, causing damages and excrement contamination (Harcourt 1957, 1963a; Sutherland 1966). All three species occur throughout North America, but with varying importance levels between regions (Harcourt 1955; Edelson et al. 1988). In southern Ontario, the study site closest to Quebec, the DBM has four to six generations per year, whereas both the ICW and the CL have three generations (Harcourt 1963a). The ICW is the eighth most important agricultural pest in Quebec, while the DBM ranks fourteenth and the CL is not regularly of concern but can be locally damaging (Chagnon et al. 1990; L. Brodeur, pers. comm.).

Control of lepidopterous pests necessitates five to six insecticide treatments per year, for a total of more than 4 000 kg of active ingredients (Chagnon et al. 1990). However, the efficacy of chemical control of these pests may decrease because of insecticide resistance (Chalfant & Brett 1965; Magaro & Edelson 1990; Vail et al. 1991), whereas public concerns on the negative impacts of insecticide residues increases (Edelson et al. 1993). Consequently, the search for alternative control methods is needed, and the use of insect parasitoids to control these pests is an avenue that our research team has decided to explore.

Despite several natural mortality factors were identified in the past, among which are introduced specific parasitoid species, their impact on pest populations is usually not sufficient to reach acceptable control levels (Harcourt 1963a; Oatman 1966; Sutherland 1966; Talekar & Shelton 1993). However, inspired by encouraging results obtained in Europe (Pak 1984; Ciochia 1990) and in the United States (Parker et al. 1971; Parker & Pinnell 1972a) with inundative releases of egg parasitoids of the genus *Trichogramma* (Hymenoptera: Trichogrammatidae), a methodology was developed in order to test this approach in Quebec (F. Fournier & G. Boivin, pers. comm.). The focus of the four years research project is to select the most promising egg parasitoids, from a collection of more than 42 species and strains of Trichogrammatidae, obtained from various parts of the world and reared in our laboratory. Concurrently to the selection tests, the seasonal occurrence and the parasitoid species associated with the three lepidopterous pests had to be studied, as these aspects were not previously determined in Quebec. This information was necessary in order to help to synchronize interventions with the targeted life stage (the lepidopterous eggs), and to evaluate the importance of naturally occurring parasitoids before any *Trichogramma* introductions are made.

The selection of the most appropriate species/strains of *Trichogramma* involves three major steps: (1) laboratory selection, (2) indoor releases on targeted plant-pest complex, and (3) experimental outdoor releases (Hassan 1993). During the selection process, only the most interesting species were retained for investigation, ending up with not more than four or five species. We measured four aspects during step (1): ease of culturing on the factitious host, *Ephestia kuehniella* (Zeller); host species preference; host age preference; and the impact of temperature on parasitism. To be retained for further experiments after the laboratory selection process, the *Trichogramma* species have to be the best ones for at least one of these attributes: they should be the cheapest ones to produce in large numbers, they have to parasitize the three pest species, they must attack eggs of any age, and they have to be active at a wide range of temperatures (Pak et al. 1990).

In the context of this biological control program, I have defined and achieved the following objectives: (1) Estimate the seasonal occurrence of the lepidopterous pests in cruciferous crops (cabbage, broccoli, and Brussels sprouts) in southwestern Quebec, and relate the occurrence of their generations to degree-days accumulations. (2) Evaluate the impact of the three cruciferous crop varieties on the abundance of the lepidopterous pests, and the relative importance of their natural enemies. (3) For the three pest species, measure the impact of egg age on the parasitism and progeny allocation of the different Trichogrammatidae species/strains.

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II. LITERATURE REVIEW

1- The cruciferous crops:

In Canada, the most important cruciferous crops actually grown are four species of the genus *Brassica*: *B. rapa, B. napus, B. campestris,* and *B. oleracea*. Rutabaga and turnip (*B. rapa*) are grown for their root; rapes (*B. napus* and *B. campestris*) are increasingly important crops that are grown for oilseed production (canola oil); finally, *B. oleracea* is the species commonly grown in a multitude of varieties such as cabbage, broccoli, Brussels sprouts, and cauliflower (Marie-Victorin 1964). These cole crops are typically grown in small plots that are plowed annually (Richard & Boivin 1994).

2- Insects associated with cruciferous crops:

During this study, I considered only lepidopterous pests of crucifers (*Brassica oleracea*). Although these are important pests, other insects have to be considered when cruciferous crops are grown. Therefore, a brief description of insect species associated with cruciferous crops is given, followed by a more detailed discussion on lepidopterous pests. In addition, I will often compare the conditions prevailing in North America with Europe, as *Brassica oleracea* and its most harmful insect pests have a Eurasian origin (Bonnemaison 1965).

Considering the arthropod community as a whole, up to 375 species were found in insecticide-free cabbage plots in southern United States (Oatman & Platner 1969), whereas 177 and 200 insect species associated with cabbage were recorded in New York and Ontario, respectively (Pimentel 1961a; Harcourt 1966). Phytophagous species, particularly the cabbage aphid (*Brevicoryne brassicae* L.), were by far the most common species found during these studies. Low numbers of predators were found, but the nocturnal insects and ground beetles were not considered.

2.1 Non-lepidopterous phytophagous insects

Most of the phytophagous insects associated with crucifers can be found almost everywhere these host plants occur. To begin with, phytophagous bugs (Homoptera: Pentatomidae) feed on crucifers in Europe, and occasionally in southern United States, but they are usually not important. Aphids (Heteroptera: Aphididae) are important pests that can transmit several viruses. The most important species are the cabbage aphid (*Brevicornis brassicae* L.) and the green peach aphid (*Myzus persicae* Sulz.). The Coleoptera most frequently found belong to the Nitidulidae, Chrysomelidae (flea beetles), and Curculionidae. Nitidulidae and Curculionidae are found on both continents and feed on buds and seed-pods, but the most serious damages are caused by the overwintering adults of flea beetles (*Phyllotreta* spp) which infest seedling crops in the spring and feed on the cotyledons and early leaves. Of the previously mentioned taxa, only aphids and flea beetles are regularly regarded as pest insects.

The cabbage root maggot, *Delia radicum* (Diptera: Anthomyiidae), occurs everywhere cruciferous crops are grown. It can be a serious threat to root crops and young plants during hot dry weather, especially for broccoli and cauliflower. Along with aphids, it is the most numerous non-lepidopterous phytophaga in Ontario (Harcourt 1966). Finally, Hymenoptera are represented by Tenthredinidae in Europe and other countries, but not in North America (Bonnemaison 1965).

2.2 Lepidoptera

2.2.1 Lepidopterous pests outside North America

Five species of Lepidoptera are commonly found on crucifers over the world. The cabbage moth, *Mamestra brassicae* L. and the cabbage looper, *Trichoplusia ni* L. (Noctuidae); the diamondback moth, *Plutella xylostella* (Plutellidae); the cabbage white butterfly, *Pieris brassicae* L. and the cabbageworm, *Artogeia (=Pieris) rapae* (Pieridae) (Bonnemaison 1965). Of these, *T. ni* is the only generalist species, and it is noxious to various other plants such as alfalfa, lettuce, beet, pea, celery, parsley, and tomato (Shorey et al. 1962). *P. brassicae* is the most abundant lepidopterous species on cruciferous crops in Europe (Bonnemaison 1965), whereas the smallest species, *P. xylostella*, has become in recent years the most destructive insect of cruciferous plants throughout the world, especially in the tropics and subtropics (Talekar & Shelton 1993).

2.2.2 Lepidopterous pests in North America

Up to 12 lepidopterous species were found on cruciferous crops in southern North America (Oatman & Platner 1969), while eight species were recorded in Ontario (Harcourt 1963a). However, only the diamondback moth (DBM), the imported cabbageworm (ICW), and the cabbage looper (CL) are usually considered as pests throughout North America. In southern regions, the CL is the most abundant species, followed by the DBM and the ICW (Edelson et al. 1988), with the cabbage webworm *Hellula rogatalis* (Hulst) is an occasional pest (Talekar 1992).

In northern North America, the ICW is usually the most abundant and destructive lepidopterous pest (Harcourt 1955). However, populations of the DBM can reach high levels, but in most years it is considered to be the least injurious pest all over North America (Harcourt 1960a). The CL can potentially be the most injurious species, but its populations are generally too sparse to be threatening in northern countries (Harcourt 1963a).

The other two lepidopterous species previously listed as important pests in Europe, *M. brassicae* and *P. brassicae*, are not yet reported in North America. However, *P. brassicae* was recently introduced in Chile (Gardiner 1974) and it would doubtless invade North America should it ever be introduced there (Courtney 1986).

In the following sections, a thorough review on the DBM, the ICW, and the CL will be presented, and the discussion will usually be restricted to North America. However, as very few information was available concerning these pests in Quebec, the most comparable information about these pests in northeastern North America were taken from studies in Ontario.

3- Diamondback moth (*Plutella xylostella*):

3.1 History, pest status

As previously stated, the DBM is the most serious insect pest of crucifers worldwide (Muckenfuss & Shepard 1994), but is only an occasional pest in northern regions (Harcourt 1986). It is believed to be the most universally distributed of all Lepidoptera (Talekar & Shelton 1993). The first North America account of the moth was in 1855 in New York (Harcourt 1955). It was accidentally introduced from Europe in North America in Illinois in

1854 and in western Canada in 1885 (USDA 1978). It then caused damage in Ontario in 1895, and in British Columbia in 1905. It has been found as far north as the North West Territories and Newfoundland (Beirne 1971).

Prior to the introduction of synthetic insecticides in the late 1940s, DBM was not reported as a major pest of crucifers. Important natural enemies were probably eliminated since then, explaining at least partly the actual pest status of DBM (Talekar & Shelton 1993). In 1953, the DBM became the first crop pest in the world to develop resistance to DDT (Johnson 1953). It also has the distinction of being the first insect to develop resistance in the field to the bacterial insecticide *Bacillus thuringiensis* (Talekar & Shelton 1993).

3.2 Biology

3.2.1 Adult life, flight, mating

The moths are inactive during the daytime and usually rest motionless on the lower surfaces of leaves of the host plant (Harcourt 1957). They are weak flyers and are readily carried by the wind. They become active just before dusk, and feed on the blossoms of nearby weeds. Mating begins at dusk on the day of emergence, and oviposition starts soon after mating (Talekar & Shelton 1993). The adult males and females live an average of 12 and 16 days, respectively (with egg-laying lasting about 10 days). Peak of flight in the night begins 90 minutes after sunset and lasts about one hour (Harcourt 1986). Conditions most favorable to flight and oviposition are high temperatures coupled with low wind velocities.

3.2.2 Oviposition

Most eggs are laid before midnight, singly, or in groups of 2 to 8, usually on the upper leaf epidermis (Harcourt 1961). Less than 1% of the eggs are laid on the stems and petioles. The eggs are very small and have a flat oval shape, 0.44 x 0.26 mm in diameter. Typically, they are laid in depressions of the leaf along the midrib and larger veins, or on the concave surfaces of the smaller veins. This habit, combined with their small size, makes them difficult to find. In addition, more eggs are laid on injured plants than on intact ones, and on or near feeding traces (Uematsu & Sakanoshita 1993). A female moth may lay up to 356 eggs during its lifetime, with an average of 159 (Harcourt 1957).

3.2.3 Larval instars behavior

The DBM goes through four larval instars and reaches a length of about 1cm. The first instar larvae mine in the spongy mesophyll tissue, whereas older larvae feed freely under the leaf surface (Talekar & Shelton 1993). The youngest (head and wrapper) leaves of cabbage were found to be preferred over older leaves (Hoy & Shelton 1987). However, the distribution of DBM larvae is variable, and one can find more larvae and pupae on frame leaves versus heads of cabbage (Lasota & Kok 1989). When disturbed, the larvae wriggle backwards very rapidly, or drop from the leaf on a fine silken thread and remain suspended (Harcourt 1957). Pupation usually takes place on the host plant. The highest activity is found during hot dry weather (Hamilton 1979).

3.3 Seasonal occurrence, number of generations

The DBM overwintering status is uncertain in southern Ontario (Butts & McEwen 1981; Smith & Sears 1982), whereas no data on this pest are available in Quebec. However, most infestations are caused by moths of southern origin, as the number of days of southerly air flow was directly related to the number of moths caught per trap in spring in Ontario (Bonnemaison 1965; Smith & Sears 1982). In southern United States, the winter crop of cabbage is harvested from March until May. In these regions, peak numbers of DBM occur there from the end of April until the first part of May (Reid & Bare 1952) during which period dispersing moths can be carried north with favorable winds (Smith & Sears 1982). Other examples of spring immigration are reported from Europe (French 1967) and Japan (Honda et al. 1992).

Four to six generations of DBM occur annually in Ontario (Harcourt 1957), while only two to three generations are reported for British Columbia (Beirne 1971). A generation can be produced in as little as 11 days (Miner 1947), and reported infestations ranged from as few as 0.08 to as many as 77 eggs per plant (Harcourt 1986).

Although not frequently reported in destructive numbers, DBM is always present and may develop rapidly from endemic to epidemic levels in northern countries (Harcourt 1961; Putman 1973). The seasonal abundance of DBM and its parasitoids has been studied in various regions of North America (Reid & Bare 1952; Pimentel 1961b; Harcourt 1963b; Oatman & Platner 1969; Harding 1976a; Latheef & Irwin 1983; Kok & McAvoy 1989; Lasota & Kok 1989; Muckenfuss & Shepard 1994). In Quebec, it is the second most important lepidopterous pest of cruciferous crops (Chagnon et al. 1990), but no published information is locally available on its development and natural enemies.

3.4 Host range

The DBM feeds mostly on members of the family Cruciferae, and it maintains itself on weeds only in the absence of more favored cultivated hosts (Talekar & Shelton 1993). However, larvae have been found feeding on 14 species of plants in south Texas, such as tomato, sunflowers (*Helianthus* spp), and wild lettuce (*Lactuca* sp) (Harding 1976a). Therefore, populations may immigrate into cabbage fields from other hosts making it difficult to predict population fluctuations in southern regions (Edelson et al. 1988).

In northern areas, the first DBM generation develops mainly on cruciferous weeds because of the lack of suitable cultivated hosts in early spring (Harcourt 1957). The yellow rocket (*Barbarea vulgaris*) is a preferred weed host, but no preference was found on cultivated crucifers (Harcourt 1986). However, mustard oil affects feeding and oviposition of insects specific to crucifers, such as the DBM (Bonnemaison 1965). Allylisothiocyanate and other agents that constitutes the sap of mustard leaves contribute to the total effect on oviposition by DBM (Thornsteinston 1960).

3.5 Plant damage

Because the tiny first instar mines the leaf tissues, it does not create much damage, whereas the final instar does most of the injury to the plants (Harcourt 1957). In addition to the leaves, mature larvae may often feed on florets of cauliflower and broccoli and bore into the heads and sprouts of cabbage and Brussels sprouts. Second to fourth instar larvae feed from lower leaf surface and usually consume all tissue except the wax layer on the upper surface, thus creating a distinctive window effect in the leaf (Talekar & Shelton 1993).

3.6 Natural enemies - parasitoids

3.6.1 Number of parasitoid species

Over the world, more than 90 parasitoid species attack DBM, and about 60 of them appear to be important (Talekar & Shelton 1993). Among these, six species attack the eggs, 38 attack the larvae, and 13 attack the pupae. Larval parasitoids are the most predominant and effective (*Diadegma, Cotesia, Diadromus*). The majority of these species came from Europe where the DBM is believed to have originated (Talekar & Shelton 1993). Five parasitoid species were reared from DBM larvae or pupae in southern North America (Oatman & Platner 1969), whereas 10 parasitoid species were reported from DBM in Ontario (Harcourt 1963a). All of the major parasitoids are specific to DBM in this region (Harcourt 1986) and none of them was reported to overwinter in Canada (Harcourt 1960a; Putman 1973).

3.6.2 Egg, larval, and pupal parasitoids

No egg parasitoids of the DBM were found in Ontario (Harcourt 1960a). Conversely, *Trichogramma* sp. is an important mortality factor in Japan (Annamalai et al. 1988), while an average of 4% of the DBM eggs were parasitized by *Trichogramma* in California (Oatman & Platner 1969).

Indigenous parasitoids, particularly *Diadegma* spp, are common in many parts of North America (Oatman & Platner 1969; Putman 1973; Harcourt 1986; Biever et al. 1992). Larvae are predominantly parasitized by an Ichneumonidae (*Diadegma insularis*) and a Braconidae (*Microplitis plutellae*). The two species are primary parasitoids of DBM (Harcourt 1960a). It is mostly the second and third instars that are susceptible to *D. insularis* and *M. plutellae* (Putman 1968). However, *D. insularis* lays its eggs in the first three instars (Harcourt 1986) and *M. plutellae* oviposits in second and third instars (Harcourt 1960a). In North America, *M. plutellae* generally ranks second in abundance to *D. insularis* (Harcourt 1960a; Putman 1973).

The Ichneumonid *Diadromus subtilicornis (=plutellae)* (Ashm.), attacks the prepupae or newly-formed pupae of DBM. It was the only pupal primary parasitoid found in Ontario (Harcourt 1960, 1963a). *Diadegma insularis* is the most abundant and important of the three species. It is also the most synchronized with its host and the only density dependent mortality factor found by Harcourt (1986). Moreover, it is intrinsically superior to the other two parasitoids (Harcourt 1963b; Bolter & Laing 1983).

The parasitoid complex of DBM on other continents is similar to that in North America: an Ichneumonid (usually *Diadegma* sp), a Braconid, and a Chalcidoid, either *Spilochalcis* or *Tetrastichus* sp (Eulophidae) are present (Horn 1987). For example, *D. insularis* is the most important parasitoid in Japan, while *M. plutellae* is of much less importance (Annamalai et al. 1988). In Australia, DBM is mostly parasitized by Ichneumonidae (*Diadegma* spp) (Hamilton 1979).

Cotesia plutellae Kurdjumov, a Braconid native to Europe, was introduced in southern United States from Hawaii against DBM larvae (Biever et al. 1994). This species was imported to Guelph in 1981 (Kelleher & Hulme 1984), but no mention of its establishment has been published.

3.7 Natural enemies - predators

Predators include arthropods like mites, spiders, and insects like Chrysopidae and Miridae (Harcourt 1960a). Predation of larvae by ants and Staphylinidae were observed in Japan (Annamalai et al. 1988). Vespid wasps were observed carrying off DBM larvae in Central America (Cordero & Cave 1992).

3.8 Diseases

In general, diseases are not a major mortality factor (Oatman & Platner 1969; Annamalai et al. 1988). However, in New Zealand, the fungus *Entomophthora spaerosperma* (Fres.) has been considered an important mortality factor (Robertson 1939).

3.9 Abiotic factors

The larvae are very susceptible to drowning on cabbage (Harcourt 1963b). They are readily disturbed by rainfall, and are washed into the leaf axils where they quickly drown in the accumulated water. In general, high mortalities are associated with thunderstorm activity and rainfall during periods of cool weather, and mortalities of up to 47% for the young larval instars have been noted. Mortality was also dependent upon the intensity of the rainfall. Mortality of gravid females due to inclement weather has been considered as the key factor in the population dynamics of the species (Harcourt 1986; Annamalai et al. 1988).

3.10 Population dynamics

The most extensive study is probably that of Harcourt (1986) in Ontario who studied the population dynamics of DBM on cabbage during an 11 year period, and compiled up to 74 life tables. Extensive mortality may occur in all stages of the insect, including the adult (Harcourt 1963b).

Despite the number of different parasitoid species found in North America, the level of parasitism usually found is of little value in controlling the DBM (Harcourt 1960a; Pimentel 1961b; Oatman & Platner 1969; Hamilton 1979). It is especially true for the first generation, as shown in a 10 years study in Saskatchewan, where the host and parasitoids densities seemed almost fortuitous initially (Putman 1973). But, in contrast to these conclusions, it was found in California that parasitization of DBM usually closely followed the larval-pupal population (Oatman & Platner 1969).

Major mortality factors of DBM in Ontario are the larval parasitoids *Microplitis plutellae* and *Diadegma insularis*, and the pupal parasitoid *Diadromus subtilicornis*. *D. insularis* is usually the dominant species (Butts 1979; Bolter 1982). However, the native parasitoids complex does not provide adequate control of DBM on Brussels sprouts late in the season when conditions favor an increase in the host population.

In conclusion, three factors are of critical importance in northern North America: weather, fecundity, and *D. insularis*. Of those, parasitoids and reduced fecundity were found the most important limiting factors. Fecundity is related to the crude protein content of the plant and declines throughout the season in successive generations each year. However, we may observe populations increasing from one generation to the other as long as hot dry weather prevails (Harcourt 1986).

4- Imported cabbageworm (*Artogeia [Pieris] rapae*):

4.1 History, pest status

The ICW is native of the Palearctic region (Gaines & Kok 1995), and was first discovered in North America in 1860 in Quebec city. In about 30 years, it had spread as far south as the Gulf of Mexico, as far north as Hudson's Bay, and west to the Rocky Mountains. It now occurs throughout most of North America (Harcourt 1963a). Life-table studies by Harcourt and his associates makes this species one of the most completely investigated of Canadian agricultural insects (Beirne 1971).

4.2 Biology

4.2.1 Adult life, flight, mating

ICW usually lives in temporary habitats such as cultivated fields (Ohsaki & Sato 1990). Feeding, dispersal, mating (and mate location), and oviposition occupy most part of the adult butterflies' life (Courtney 1986). Most ICW females are mated within 24 hours of emergence (Jones 1977) and they begin to lay eggs 24-36 hours after mating. Newly emerged females ICW always disperse from their larval habitat (Ohsaki & Sato 1990). However, most or all of a female's daily complement of mature eggs is laid on the first patch of hosts that she finds on that day (Jones 1977; Fahrig & Paloheimo 1988). Only 15 min is required, on average, to lay the total daily number of mature eggs (Fahrig & Paloheimo 1988). However, eggs are spread over the entire host plant patch (Root & Kareiva 1984). The female butterfly may live an average of 20 days (Gossard & Jones 1977), and lay an average of 356 eggs (Richards 1940).

Most of the flight time is spent in non hostpatch areas, feeding on nectar, and searching for new host patches (Fahrig & Paloheimo 1988). Flight direction is highly directional within a particular day, but changes at random from one day to the next (Jones et al. 1980). The butterflies tend to fly against the wind (Beirne 1971). When searching for host plants, females fly close to the vegetation, stopping every few meters to test the suitability of plants for egg laying (Root & Kareiva 1984). Butterflies disperse large distances in random directions from patches, and do not detect patches from a distance (Fahrig & Paloheimo 1988). One female butterfly flies about 700m per day (Jones et al. 1980).

4.2.2 Oviposition

ICW is an enormously successful invader, capable of attaining average densities of more than 80 eggs per host (Jones & Ives 1979; Root & Kareiva 1984). Recognition of host plants by ovipositing ICW depends on the presence of water-soluble, nonvolatile chemical stimulants that are detected by tarsal chemoreceptors upon contact with the plant surface (Renwick & Radke 1983). More than one chemical are likely involved in the process of host plant recognition. ICW females prefer to lay eggs in open, sunny sites (Cromartie 1975a). In northeastern North America, the ICW principal wild hosts, *Barbarea vulgaris* and *Lepidium virginicum*, are plants of open, sunny successional habitats and roadsides (Cromartie 1975b).

ICW females lay most of their eggs within a one mile radius, but marked individuals were shown to oviposit up to five miles from a butterfly release site (Parker 1970). The eggs are laid singly on the outer leaves of the cabbage plant, with approximately 70 % of them on the lower leaf epidermis (Harcourt 1962). Furthermore, the border rows of the crop invariably receive more eggs than do those that are centrally located (Harcourt 1962). Larger plants and older leaves are preferred for oviposition, though the oldest are sometimes avoided (Ives 1978).

Discrimination amongst host varieties is poor and bears little relation to suitability for larval growth, whereas larger plants receive more eggs than smaller ones of the same cultivar, but cultivar preferences may override the response to size (Ives 1978; Jones & Ives 1979). Cultivated host plants are much preferred over wild host plants (Jones & Ives 1979). Finally, ICW do not discriminate against plants already bearing eggs or larvae, unless larval feeding damage to the plant is severe (Ives 1978). The rate of egg-laying is markedly influenced by the weather, and ICW oviposits mostly on warm sunny days (Gossard &

Jones 1977). The yellow eggs of the ICW are shaped like a bullet, 1.01 x 0.44 mm in size, and vertically striped (Pak et al. 1986).

4.2.3 Larval instars behavior

The ICW has five larval instars. The location of early instars is related to the oviposition behavior of females (Ives 1978). On cabbage, the larvae remain on the outer older leaves during the first two instars, and feed from the lower leaf epidermis, near the site of oviposition (Harcourt 1962). After the second molt, they move to the central parts of the plant to feed on the head and wrapper leaves (Dempster 1969).

Late instar larvae (instars three to five) prefer young leaf tissue (Hoy & Shelton 1987) and tend to feed on the upper leaves of the plants, causing changes in both plant structure and the rate of plant growth (Samson & Geier 1983). Larval distributions on host plants vary with larval density, while the rate of larval feeding depends on the size and the age distribution of the pest population, temperature, and the condition of the host plant. The fully grown larva often leaves the plant to pupate (Dempster 1969), or pupation occurs on the undersurface of the lower leaves (Harcourt 1966).

4.3 Seasonal occurrence, number of generations

In northern parts of North America, the ICW flies northward every year, especially at times of high pressure, on the hot, strong southerly winds. An infestation may originate from a population that survived the winter as pupae or from one that migrates from elsewhere or from a combination of both. For this reason, it would be difficult to predict the occurrence and intensity of outbreaks (Beirne 1971).

The seasonal activity and number of generations of ICW vary considerably across North America because of the broad range of latitudes, climates, and elevations (Gaines & Kok 1995). Four to five generations are found in southern Virginia, while as many as six distinct generations per year were observed in Missouri and California (Oatman 1966; Parker 1970; Gaines & Kok 1995).

The first brood of ICW in northern countries depends mostly on wild hosts because cultivated crucifers are unavailable when the eggs are deposited in April or early May

(Sutherland 1966; Root & Tahvanainen 1969). There is an average of three generations per year in Ontario, the winter being spent as a pupa (Harcourt 1962, 1966a). Similarly, three to four generations have been found in England (Richards 1940). The development of ICW on cruciferous crops in Quebec is probably comparable with Ontario, but studies are needed to clarify the situation.

4.4 Host range

The host range of ICW is restricted to crucifers and plants within a few other families that are characterized by the presence of glucosinolates (Renwick & Radke 1983; Huang & Renwick 1993). However, some crucifers, such as *Capsella bursa-pastoris* and *Cheiranthus* spp, contain oviposition deterrents (Richards 1940; Renwick & Radke 1987), whereas the larvae refuse to feed on the tender leaves of *Raphanus raphanistrum* L., *Sinapsis avensis* L., and *Brassica campestris* L. (canola) (Blunck 1957). *Babarea vulgaris* is the principal wild host of ICW in New York state (Root & Tahvanainen 1969).

Latheef & Irwin (1979) found that preference for different cabbage cultivars was not definitive and temporal variation occurred as the season progressed, mainly because of size differences. This is in agreement with Radcliffe & Chapman (1965) who reported that leaf surface was a factor in the susceptibility of different varieties. Probably far more eggs are laid on cabbage crops than on any other plant (Latheef & Irwin 1979).

4.5 Plant damage

Most consumption of food occurs in the last instar. Late instars ICW commonly feed at the leaf margins, particularly on the developing center leaves of young crucifers. This feeding is severe; as leaves expand, notches and holes similarly enlarge (Sutherland 1966). Moreover, the combination of feeding and contamination with excrement can make a whole field unmarketable. Turnip fields have been virtually defoliated by ICW larvae (Beirne 1971).

At low temperatures, the damage by ICW can be partly compensated by the growth rate, as the plant has a lower threshold than the larvae (0°C compared with 10°C) (Samson & Geier 1983). The form of the host plants may also influence the damage caused and the degree of natural control by parasitoids. Pimentel (1961a) in New York reported that there were more caterpillars on plants of Brussels sprouts and cabbage that form a head, than on the broccoli, collards and kale that form no head.

4.6 Natural enemies - parasitoids

4.6.1 Number of parasitoid species

The parasitoid complex of ICW is remarkably constant throughout the world, partly because parasitoid species specific to this pest have also been introduced. Usually, one or two Braconids (*Cotesia glomerata* and *C. rubecula*), some generalist Tachinids, and one Chalcid (*Pteromalus puparum*) are recorded from ICW larvae and pupae.

At least six species of parasitoid were found in Ontario (Beirne 1971). On the west side of the continent, four species of parasitoids were found in the coastal area of British Columbia (Wilkinson 1966). Sutherland (1966) found four species in Long Island, New York, while nine species were reared from ICW larvae or pupae in California (Oatman & Platner 1969). In Europe, four parasitoid species were reported in England (Dempster 1969).

C. glomerata and *P. puparum* were introduced in North America by the end of the last century (Hamilton 1979). Until recently, *C. rubecula* had not been introduced, and *C. glomerata* had a much greater importance in North America than in Europe (Blunck 1957; Le Masurier & Waage 1993).

4.6.2 Egg parasitoids

When egg parasitoids are considered in studies on ICW mortality factors, they are usually found to have little impact, if any, on the host populations (Richards 1940; Bonnemaison 1965; Harcourt 1966; Dempster 1969). However, egg parasitoids like *Trichogramma* spp may be important in population dynamics of the ICW and have proved to be useful biological control agents (Stern & Bowen 1963; Parker 1970; Parker & Pinnell 1971; Parker et al. 1971; Oatman & Platner 1972).

In North America, naturally occurring *T. pretiosum* Riley were reared from ICW eggs in California (Oatman 1966), whereas no egg parasitoid was found in Ontario

(Harcourt 1966). In California, *T. evanescens* Westwood was introduced from Europe in 1966 (Oatman et al. 1968) and parasitism rates reached up to 77% (Bonnemaison 1965). Attempts to control the ICW in North America by introducing *Trichogramma* are treated in more details in section 8.

4.6.3 Larval parasitoids

Diptera

Diptera parasitoids of ICW larvae rarely account for more than 10% of the total parasitism, with two Tachinid flies being the most important ones. *Phryxe vulgaris* (Fall.) is polyphagous and attacks fourth and fifth instar ICW larvae (Richards 1940). *Compsilura concinnata* (Mg.) is another extremely polyphagous Tachinid parasitoid which lays its eggs in the gut of the host, but it is of much less importance (Richards 1940; Harcourt 1963a). *Phryxe vulgaris* is apparently the most common Tachinid parasite of ICW in the northern part of United States and in Canada, as well as in England, where it is probably native (Moss 1933; Richards 1940). Tachinids are usually not important, but it appeared that they were the most important parasitoids of ICW larvae in southern California (Oatman 1966).

Hymenoptera: *Cotesia (=Apanteles) glomerata*

In Europe, *C. glomerata* is essentially a parasitoid of *Pieris brassicae* and only secondarily attack ICW (Richards 1940), whereas the populations of *C. glomerata* established in North America (where *P. brassicae* does not occur) attack the ICW at a higher rate (Le Masurier & Waage 1993). It is a gregarious parasitoid that deposits 15 to 35 eggs at one insertion of the ovipositor (USDA 1978). This Braconid was introduced into North America from England in around 1863, but releases led to establishment only in 1884, near Washington (Clausen 1956; USDA 1978). *C. glomerata* may not be an effective parasitoid of the larva during the spring because of asynchronization, encapsulation, and hyperparasitism (Parker 1970). Most eggs of *C. glomerata* are encapsulated when laid in late second to fifth instar (Parker 1970; Brodeur & Vet 1995), and little or no attack occurs on second or third instars in a field survey (van Driesche 1988). Measuring field population recruitment of ICW, van Driesche (1988) found that *C. glomerata* attack rate increased with larval density. Its biology is reviewed by Laing & Levin (1982).

Hymenoptera: *Cotesia (=Apanteles) rubecula*

This solitary Braconid is native to Europe and United Kingdom. It had not been reported in North America (Blunck 1957) prior to its discovery in British Columbia in 1963 where it was apparently accidentally introduced (Wilkinson 1966).

C. rubecula was obtained from British Columbia and introduced in the United States in California, Missouri, New Jersey, and Hawaii, during 1967-1968 (USDA 1978; Puttler et al. 1970). But, despite releases of the parasite, it did not establish in most cases (Puttler et al. 1970). Several attempts to colonize other North American localities with Vancouver stock have failed (Oatman & Platner 1969; Oatman & Platner 1972; Corrigan 1982). In southern United States, the potential for *C. rubecula* to reduce populations of ICW has been demonstrated, but continual releases must be made (Parker & Pinnell 1972b).

Until recently, *C. rubecula* has not been reported at other southern release sites in the United States (Puttler et al. 1970). It was not found in Virginia, while it occurred in Washington and Oregon, but seemed to be limited farther south in Oregon due to its diapause characteristics (Chamberlin & Kok 1986; Biever 1992). *C. rubecula* may enter diapause prematurely while ambient temperature are still warm and thus it would not be able to survive the obligatory diapause period. More recently, a Yugoslavian strain was released and successfully established in Michigan and Virginia (McDonald & Kok 1992).

Ottawa is probably the coldest of the release sites (Nealis 1985), and it has been recovered there in 1982, 10 years after its release (Corrigan 1982). D.G. Harcourt released the parasites from a culture started from individuals collected in southern British Columbia. Releases took place in 1970-1971 and in 1978-1979. A second strain of *C. rubecula* from north eastern China was released at Guelph in 1982 (Kelleher & Hulme 1984) and more recently in Massachusetts (Roy van Driesche, pers. comm.).

Although oviposition is proved to occur in all larval instars of ICW, successfully parasitized larvae beyond the third instar were not found (Parker & Pinnell 1973; Nealis et al. 1984; Sengonca & Peters 1993). This is due to a higher egg encapsulation rate in older than in younger larvae (Parker & Pinnell 1973; Brodeur & Vet 1995). The parasitism of larvae can reach 90% and, like its host, *C. rubecula* enters diapause in fall (Bonnemaison 1965; Nealis 1985).

Comparison of *C. glomerata* and *C. rubecula*

Among the parasitoids of ICW, *C. glomerata* and *C. rubecula* are probably the most interesting cases. They both compete for the same host stages, but their specificity, life history, and their effect on host development are quite different, as well as their introduction history (see above).

C. rubecula is more specific to ICW than *C. glomerata* (Blunck 1957), which is primarily a parasite of *Pieris brassicae* (Puttler et al. 1970). Interestingly, LeMasurier & Waage (1993) showed that attack rates (with ICW) of a population of *C. glomerata*, taken from Massachusetts (where *P. brassicae* does not occur), were superior to that of a British population. However, *C. rubecula* was still superior to both *C. glomerata* populations. The specificity of *C. rubecula* to ICW habitat is furthermore supported by the attraction of the parasitoid for host-infested plants (Geervliet et al. 1994; Kaiser et al. 1994), and to cabbage previously infested, frass, and regurgitate of ICW (Agelopoulos & Keller 1994).

Both *C. rubecula* and *C. glomerata* slow the development of their host, but the former emerges out of its host from fourth instar larvae and the latter from the fifth instar (Nealis et al. 1984). However, most consumption of food by the ICW larva occurs at the last instar. Thus, larvae parasitized by *C. glomerata* consumes more leaf area than normal larvae, which in turn consumes more leaf area than those parasitized by *C. rubecula*. The difference is enormous: those larvae parasitized by *C. glomerata* can eat 10 times more cabbage leaf than larvae parasitized by *C. rubecula* (Rahman 1970; Parker & Pinnell 1973).

4.6.4 Pupal parasitoids

Pteromalus puparum is a well-known Chalcid parasitoid of many butterfly pupae (Richards 1940). This gregarious polyphagous species (Parker 1970) has been introduced accidentally in North America in the late 1800's (Oatman 1966), some time before *C.*

glomerata. Both became generally distributed in the United States and Canada (Clausen 1956).

Up to 75% of ICW pupae were found parasitized by this parasitoid in Virginia (Chamberlin & Kok 1986; Lasota & Kok 1986). In Montreal and surrounding areas, Blunck (1957) found that pupae of ICW were effectively parasitized by *P. puparum*. It has a good searching ability at high host densities (Hassan 1976).

4.6.5 Hyperparasitoids

In Europe, the most important hyperparasitoid is *Tetrastichus galactopus (=rapo)* (Walk), a gregarious Eulophidae that attack *C. rubecula* and *C. glomerata* inside the ICW larva (Corrigan 1982). It oviposits directly into the primary parasite through the body wall of the primary host, and it is incapable of parasitize once its host has formed a cocoon (Richards 1940; Nealis 1985).

Several hyperparasitoid species were found in North America, attacking mostly *Cotesia* spp. Parker (1970) found twelve species of hyperparasitoids on *C. glomerata*, while six of these species were reared from *C. glomerata* cocoon by Parker et al. (1971) in Missouri. Up to 100% of the *C. rubecula* cocoons collected were hyperparasitized. Several *C. rubecula* were parasitized by *T. galactopus* (Chamberlin & Kok 1986), and up to 40% *C. rubecula* cocoons were parasitized after its introduction in Virginia in 1987 (McDonald & Kok 1992). These hyperparasitoids may in part be responsible for the introduction failures of *C. rubecula* stated in previous sections. However, apart from *T. galactopus*, hyperparasitoids are not reported in high numbers in northern regions (Blunck 1957; Nealis 1983; McDonald & Kok 1992).

4.7 Natural enemies - predators

Very few population studies on ICW has considered arthropod predation to be of any importance (reviewed by Dempster (1969)). Predators are given little consideration because few are to be found during the day, and those occurring on the plant are mainly aphid predators (e.g. Syrphidae, Chrysopidae, Coccinelidae). Only by using a technique such as the precipitin test as described by Dempster (1969) can the full effect of arthropod predators be appreciated. Dempster (1967) and Ashby (1974) studied ICW predation using this method and felt that Syrphid larvae, Carabidae, and Phalangidae were the most important arthropod predators (in Courtney 1986).

Predation of the ICW by arthropods is mostly restricted to eggs and small larvae (Dempster 1969). During a study in Missouri, predators killed more eggs of ICW than any other agents (Parker 1970). Numerous predators were observed feeding on ICW eggs: ants, *Chrysopa* larvae, predaceous mites, *Lygus* adults and nymphs, Coccinellid adults and larvae. Predation was also the most important cause of pupal mortality: wasps (*Polistes* and *Vespula*), ants, Pentatomids, Phalangids, beetles, Carabids, and Cantharid larvae (Dempster 1969; Parker 1970). In England, ICW eggs and young larvae are far more destroyed by predators on the wild crucifers than on cabbage (Richards 1940). Finally, bird predation may be substantial when the plot is located near a forest edge, but its effects are restricted to the larger ICW larvae (Dempster 1969).

4.8 Diseases

The majority of Lepidoptera are very susceptible to virus, bacteria, and fungus diseases. The ICW is attacked by granulosis and polyhedrosis virus as well as by bacteria, microsporidium, and fungus (Bonnemaison 1965). The most common is a granulosis viruses, that can be an important mortality factor, especially at high larval densities. The fungus *Metarrhizium anisopliae* Sorokin, the so-called green muscadine fungus, has been found but was considered as rare (Dempster 1969). Interestingly, microsporidian parasites are common in Europe, but only occasional in North America (Blunck 1957).

The transmission of the virus infection is promoted by the caterpillar behavior of moving to the central part of the plant during third to fifth instars (Harcourt 1966). The body of dead infected larvae quickly liquefy and the virus particles may accumulate on foliage or in the soil. In addition, the granulosis virus can be transmitted to ICW larvae by *C. glomerata* (Levin et al. 1983). The adult females may transmit the virus to its host in two ways: by being infected by previous ovipositions, or if adult females emerge from virus infected larvae. *C. glomerata* and the virus compete for their mutual host, but survival of the parasitoid is possible if oviposition precede exposure of ICW larva to the virus (Levin et al. 1981).

The occurrence of ICW virus diseases in North America is irregular. Some studies reported more than 50% of virus-diseased larvae (Chamberlin & Kok 1986), whereas some others never reported significant loss of ICW caused by virus (Parker 1970).

4.9 Abiotic factors

The young larvae are invariably on the underside of the outer leaves and are extremely difficult to dislodge. However, during heavy rainfalls, the small caterpillars are dislodged and some are drown in the leaf axils. Compared with cabbage (Harcourt 1966), young larvae drowning did not appear to be an important cause of mortality on Brussels sprouts (Dempster 1969). Rainfall can be the major mortality factor during first and second instars, whereas adults may be killed by heavy rains (Harcourt 1966; Ohsaki 1979). Bad weather can result in low egg deposition (Parker 1970). Furthermore, cold weather as well as chemicals (pesticides, fertilizers) can cause stress, and this stress can cause viral epidemics in ICW (Biever & Wilkinson 1978; Jaques & Laing 1978).

4.10 Other factors

As pointed out by Dempster (1983), cannibalism is one of the density-dependent mortality factors demonstrated for ICW (Jones & Ives 1979). Critical observations are that many butterflies larvae, such as the ICW, eat their own eggshell immediately upon emergence (Courtney 1986). Cannibalism, usually of unhatched eggs, is the major form of interference.

The importance of the larval host-plant as direct (inability to eat the host) or indirect (differential parasitism on different plants) cause of death is almost certainly heavily underestimated (Coutney 1986). For example, Loader & Damman 1991 found that ICW larvae developed more slowly and devoted more of their time to feeding on low-nitrogen collard plants than on high-nitrogen plants. This was related to higher predation of ICW larvae on low-nitrogen plants, while *Pteromalus puparum* was found more frequently on high-nitrogen plants.

4.11 Population dynamics

An insect which, like ICW, lays 300-400 eggs must have about 99% of each generation killed if the species is not to increase (Richards 1940). Moreover, with such high egg numbers, a decrease of 1% in the death rate means that the species will start the next generation with the population three times as dense.

Because of their wide distribution and the ease with which all stages of the insect can be followed, population dynamics of the ICW and other Pierid butterflies have been well studied and were used as models to explain lepidopterous way of life (Courtney 1986). Of great interest is the replication of such studies over a wide geographical range and over many generations. Fundamentally similar patterns of survival are obtained in different times and places. Typically, mortality of eggs is low, of early instars rather high, of middle instars again low, until parasitoids kill many late larvae and pupae (Harcourt 1962).

The most extensive work on the natural mortality of ICW is that of Harcourt (1966a). Life tables analysis were compiled from 18 generations data collected in eastern Ontario during summers of 1959 to 1964. He found that *C. glomerata* parasitism was very low, with an average rate below 1%, while *P. vulgaris* showed an average parasitization rate of 13%. *P. puparum* attacked ICW pupae with an average rate of 17%. The three parasitoids are monophagous in eastern Ontario.

No evidence of egg parasitism was found during these studies, and loss of eggs through the action of weather was negligible (Harcourt 1962). From life table analysis, larval mortality factors were divided into three periods. For period one (from hatching to middle third instar), no mortality was caused by parasitoids, while the arthropod predators were not important, and rainfall caused considerable mortality because larvae were drown in water trapped into the leaf axil of cabbage. In period two (from middle third instar to middle fifth instar), the mortality caused by parasitoids and predators is the same as previous. However, the migration of the larvae to the central parts of the plant resulted in their exposure to a density dependent granulosis virus.

During the third period (from middle fifth instar to pupation), mortality factors were as in period two, plus the mortality caused by *C. glomerata* which emerged and killed the larva during the fifth instar. Finally, mortality of the pupae was found to be caused mostly by the Tachinid *Phryxe vulgaris*, the Chalcidoid *Pteromalus puparum*, and diseases. On the other hand, evidence of mortality due to arthropod predators was not observed, and predation by birds was evident only in the fall.

Age, size, species, and variety of host plants have all been shown to influence larval development and survival; and the risks of cannibalism, competition for food, and focusing of predators and parasitoids presumably make plants already bearing eggs or larvae more hazardous for later oviposition (Ives 1978). Whether there is heterogeneity within a host plant in terms of suitability for larval development and survivorship is not known (Courtney 1986).

5- Cabbage looper (*Trichoplusia ni*):

5.1 History, pest status

The CL was described in the United States in 1870 (Sutherland 1966). In Ontario, it was recorded in 1935, and almost annually since, with important damage one year out of three. It is a widespread, polyphagous, and often highly destructive species (Oatman & Platner 1969). However, it is often the least important lepidopterous species in northern countries (Pimentel 1961b), and it is the least studied of the three major lepidopterous pests of cruciferous crops.

5.2 Biology

5.2.1 Adult life, flight, mating

CL moths become active shortly after sunset, and usually feed and deposit their eggs about dusk, though daylight activity has been observed in cloudy weather or during cool evenings (Shorey et al. 1962). Mating usually occurs after midnight but not before the second night, and the mature eggs are not found in the oviducts until two days after emergence. The CL moths may live an average of 16 days for females, and 17 days for males (Sutherland 1966).

5.2.2 Oviposition

CL eggs are generally laid singly or in groups of 2 to 11, usually near the margin and on either sides of the leaves, with up to 91% of the eggs being laid on the lower leaf surface (Harcourt 1963a; Sutherland 1966). Normally, a female CL lays 275 to 350 eggs during its lifetime (McEwen & Hervey 1960). The eggs, roundly shaped (0.6 mm diameter x 0.4 mm height) are creamy white and vertically striped (Sutherland 1966).

5.2.3 Larval instars behavior

The CL larvae crawl by doubling up to form a loop, then projecting the front end of the body forward (Harcourt 1963a). Similarly to the ICW, the larvae disperse, starting in the third instar, from frame leaves toward the wrapper leaves and head, whereas pupation occurs on frame and old or dying leaves at the base of the plant (Sutherland 1966). The vast majority of CL larvae are found on the lowest leaves on the plant (Hoy & Shelton 1987; Hoy et al. 1989).

However, in contrast with ICW, CL larvae are believed to prefer feeding on the underside of the oldest leaves of cabbage, and avoid the highest concentrations of apparently protective secondary compounds (Broadway & Colvin 1992). On cabbage, Lasota & Kok (1989) found that more CL larvae and pupae were present on frame leaves compared with heads. Finally, in an original experiment, Hoy et al. (1989) followed movements of CL larvae (previously fed with radio-isotopic diet) with a Geiger counter, and observed that larvae respond to low temperatures and high vapor pressure deficit by moving upward toward the wrapper leaves and cabbage heads. Conversely, larvae moved down to the shaded, cooler, lower parts of the plant during high temperatures and low vapor pressure deficit.

5.3 Seasonal occurrence, number of generations

The CL does not overwinter in areas north of South Carolina (Sutherland 1966; Elsey & Rabb 1970; Chamberlin & Kok 1986). Therefore, in northern areas, populations are believed to originate from southern regions from where the moths immigrate.

In warm areas, the relative abundance of the caterpillars is quite different from that found in the North. It is often the dominant lepidopterous species in southern regions, followed by the ICW and the DBM (Harrison & Brubaker 1943; Latheef & Irwin 1983; Kok & McAvoy 1989). Up to six generations occur during a year in southern United States (Oatman 1966), whereas three generations are observed in Ontario (Harcourt 1963a).

Numbers of CL on crucifers, particularly near its northern limit, vary tremendously from year to year (Harcourt et al. 1955). CL populations appear to build up to higher levels during hot, dry years (Hofmaster 1961; Sutherland 1966). As opposed to the ICW and the DBM, wild crucifers do not appear to be a food source for early season CL. At harvest, the CL is often the most abundant species in New York cabbage (Andaloro et al. 1982), and it is also the most difficult species to control (Eckenrode et al. 1981). It is a sporadic pest in Ontario and Quebec, but is not sufficiently abundant in most years to constitute an economic problem (Harcourt 1960b, 1963a). The CL at no time formed a significant portion of the species complex on either early and late cabbage during Harcourt et al. (1955) study in Ontario.

5.4 Host range

CL feeds on at least 119 species, varieties and cultivars of plants in 29 families, but favors cultivated crucifers. Among the other common cultivated hosts for CL, the larvae feed on lettuce, cucumber, tomato, potato, pepper, lima bean, chrysanthemum, watermelon, alfalfa, and cotton (Harding 1976b; Soo Hoo et al. 1984). Preference between cruciferous crops has rarely been investigated for this species, but a preference for oviposition on broccoli over cabbage was observed by Sutherland (1966).

5.5 Plant damage

As for the ICW, most damage is done during the last larval instars, while damage distribution over the plant is more variable. Larvae usually do not feed at the leaf margin, as opposed to the ICW (Sutherland 1966).

5.6 Natural enemies - parasitoids

5.6.1 Number of parasitoid species

In North America, the parasitoids of CL are mostly Hymenoptera, and up to 11 species are found, restricted to three families: Encyrtidae, Ichneumonidae, and Trichogrammatidae (Sutherland 1966; Oatman & Platner 1969; Martin et al. 1981). In addition, three species of Diptera (Tachinidae) were found, with *Voria ruralis* (Fallen) usually being the dominant parasitoid of CL (Sutherland 1966). Important parasitoid species of eggs, larvae and pupae include Hymenoptera such as *Copidosoma truncatellum* (Dalman), *Hyposoter exiguae* (Viereck), and *Pediobius* sp, respectively. In Canada, the CL larvae are attacked by a polyhedral virus and by four species of parasitoid: *C. truncatellum*, *Itoplectis conquisitor* (Say), *Compsilura concinnata* (Mg.) and *Stenichneumon culpator cincticornis* (Cress.) (Harcourt 1963a; Beirne 1971).

5.6.2 Egg parasitoids

Naturally occurring parasitoids of CL eggs are commonly found in North America, but usually low levels of parasitism are found. Three species of *Trichogramma* were found to parasitize CL eggs in cruciferous crops: *T. pretiosum*, *T. minutum* and *T. exiguum* (Sutherland 1966; Oatman & Platner 1969; Elsey & Rabb 1970; Chamberlin & Kok 1986). In southern North America, parasitization of CL eggs in cabbage is generally above 10% and as high as 55% (Martin et al. 1981). In addition, a strain of *T. evanescens* obtained from Europe was introduced in southern California during 1965-1967 (Oatman et al. 1968).

The polyembryonic Encyrtidae *Copidosoma floridanum (=truncatellum)*, which lays its eggs within those of the host and completes its development when the host attains the prepupal stage, is also regularly reported (Pimentel 1961b; Oatman & Platner 1969; Martin et al. 1981; Kok & McAvoy 1989). It is usually the most important egg parasitoid of CL, and as many as 1124 specimens were reared from a single host collected in Ontario (Harcourt 1963a).

5.6.3 Larval and pupal parasitoids

Throughout southern and northwestern North America, the only larval parasitoid commonly recovered from CL is the Tachinidae *Voria ruralis* (Fallen) (Oatman 1966; Jackson et al. 1969; Elsey & Rabb 1970; Chamberlin & Kok 1986; Biever et al. 1992). However, this Tachinid was not reported in north eastern regions like New York (Pimentel 1961b) and Ontario (Harcourt 1963a). Hosts of *V. ruralis* are larvae of the family Noctuidae (Jackson et al. 1969). Oatman & Platner (1969) listed the Braconid *Microplitis brassicae* as an important mortality factor of CL in California, but *V. ruralis* still was the dominant species. Ichneumonidae, like *Hyposoter exiguae*, may occur at low numbers but never represent an important mortality factor. Harcourt (1963a) listed three other parasitoid species in Ontario: the Ichneumonidae *Itoplectis conquisitor* (Say), *Stenichneumon culpator cincticornis* (Cress.), and the Tachinid *Compsilura concinnata* (Mg).

5.7 Natural enemies - predators

The identity and importance of CL predators is poorly known, and most reports are based on limited observation or association. The predators of CL are generally the same as those observed attacking DBM and ICW (Sutherland 1966; Elsey & Rabb 1970).

5.8 Diseases

Field populations of CL are frequently destroyed by a polyhedrosis virus (Harcourt 1963a). The virus disease was found in most parts of the United States (Pimentel 1961b; Oatman & Platner 1969; Elsey & Rabb 1970), and Canada (Beirne 1971). The first report of the polyhedrosis virus from Canada was in 1959, and the diseased larvae were found in eastern Ontario and southwestern Quebec (Harcourt 1960b).

5.9 Abiotic factors

Although the impact of inclement weather on the mortality of the different stages was never measured, it is likely that it would strongly affect the oviposition behavior. However, temperature may interact with virus disease as cool, wet weather seemed to increase the impact of the disease (Elsey & Rabb 1970).

5.10 Population dynamics

The general aspects of CL biology are well known, but its population dynamics are poorly understood. Life tables were constructed by Elsey & Rabb (1970) from CL on collards in North Carolina. *Trichogramma* species were found, but egg mortality was of little importance in the population dynamics of CL. It was concluded that the disease and parasitism were the major mortality factors of larvae.

The climate and the presence of polyhedrosis virus have considerable influence on CL. The virus is highly infective and pathogenic to CL, and it was found to be one of the prime factors limiting the density of caterpillars in New York (Pimentel 1961b).

6- Chemical control of lepidopterous pests:

Application of chemical insecticides to *Brassica* crops has been the major management tool for controlling insect pests (Andaloro et al. 1983). However, recent public concern about the use of the synthetic organic insecticides and their effects on human health and the environment has resulted in a demand for vegetables grown without the use of these materials (Edelson et al. 1993). Additionally, by the sixties, DBM and CL populations in North America have become resistant to some insecticides (Chalfant & Brett 1965; Magaro & Edelson 1990; Vail et al. 1991). Furthermore, resistance of DBM to *B. thuringiensis* subspecies now occurs in the field (Shelton et al. 1993). Therefore, alternative management tools are being developed (Endersby & Morgan 1991).

The regular use of chemical pesticides tends to deplete the valuable resource of pest susceptibility (Samson & Geier 1983). This might tend to promote the buildup of pest populations by causing virus-infected larvae to fall to the ground before the virus particles are released (Beirne 1971). The negative impact of chemical insecticides on parasitoids of DBM, such as *D. insulare*, is also well documented (Schalk et al. 1993; Muckenfuss & Shepard 1994).

Problems with complete reliance on conventional insecticides include the development of insect resistance, secondary pests resurgence, and environmental contamination (Hough & Hahn 1992). These problems had led to the development of pest management programs that usually begin by insect monitoring used to help synchronize insecticides applications with the populations of the pests, followed by research on alternative biological or non-chemical control methods, and ultimately by the use of all available methods in an integrated pest management program (see below).

7- Biological control of lepidopterous pests:

7.1 Biological control agents

7.1.1 Pathogens

A fungal pathogen (Zygomycetes) had been used with some success against the DBM in a field trial in UK, but this method requires high humidity, which is a potential limitation for its use. (Pell & Wilding 1994).

A granulosis virus of ICW is known to be highly infective. In southern Ontario, before being artificially introduced or applied to fields, viruses of CL and ICW were widespread (Jaques & Harcourt 1971). It was concluded that the residues accumulated naturally from cadavers of virus-killed host insects. Virus can retain activity five years after application to soil, thus resulting in prolonged effect of applications. The combination of ICW and CL viruses with chemical insecticides was found to be especially effective (Jaques 1972; Kelleher & Hulme 1984). Although viruses can potentially control populations of ICW and CL, they are not commercially used because of registration limitations and public concerns.

Several BC agents are commercially available against lepidopterous pests, mostly from California (Flint 1993; Cranshaw et al. 1996). Such products as micro-organisms are registered and sold as pesticides, the most common being *B. thuringiensis*. The biorational (*B. thuringiensis*) and synthetic organic insecticides were equally effective in controlling lepidopterous pests on broccoli in southern Texas, but the use of *B. thuringiensis* required a greater number of applications for effective control (Edelson et al. 1993).

In Canada, *B. thuringiensis* is available to producers (Kelleher & Hulme 1984). The few growers that use this method of control usually obtain good control (Chagnon et al. 1990). However, resistance of lepidopterous pests to different formulations of *B. thuringiensis* is now occurring (Shelton et al. 1993). Combining the viruses of CL and ICW with *B. thuringiensis* enhanced effectiveness, and effectiveness is further enhanced by addition of low dosages of insecticide (Jaques & Laing 1978).

7.1.2 Natural enemies

The nematode, DD136 (Steinernematidae), which develops in the intestine of insects, has been field tested against ICW and CL, and a high mortality was observed (Welch & Briand 1960). However, by 1980, most work on use of nematodes had ceased although there are still several avenues to explore (Kelleher & Hulme 1984). But it should be noted that nematodes are being evaluated in the course of a research project in Quebec (G. Bélair, pers. comm.).

Most of the parasitoid and predator introductions in North America have already been discussed in previous sections. None has proved to achieved economical control on a regular basis without repeated inundative releases. However, all possibilities have not yet been looked for (see section 10). In Canada, introductions of BC agents that were made from 1959 to 1980 are summarized in Commonwealth Agricultural bureaux (1971) and Kelleher & Hulme (1984).

8- The Trichogrammatidae:

An IPM program is currently at an early stage of development in Quebec. On one side, field scouting methods are developed and tested by extension personnel (L. Brodeur, pers. comm.). Concurrently, alternative methods to insecticides are being investigated to control the three lepidopterous species. The principal objective of this project is to select the most appropriate species or strains of egg parasitoids to be used for inundative releases (see below). Ultimately, we hope to replace the use of insecticides in cruciferous crops with carefully synchronized releases of locally-produced egg parasitoids, which could be used in combination with other control agents such as *B. thuringiensis* and nematodes.

8.1 Description

All species of the family Trichogrammatidae (mainly *Trichogramma* and *Trichogrammatoidea*) are primary parasitoids of other insect eggs, mostly Lepidoptera

(Olkowski & Zhang 1990). These parasitic wasps are the most widely studied biological control agents in the world. The advantage of using egg parasitoids in BC over larval parasitoids is that the former prevent hatching of their hosts. Furthermore, egg parasitoids can be mass reared in large numbers more easily than larval parasitoids, and on low cost factitious hosts (Hassan 1993). This ease of producing *Trichogramma* allows us to release it in sufficient numbers on target crops in order to have an immediate impact on the host population. As a result, the permanent establishment of the parasitoid in the field is not necessary for the successful control of the pests, a condition that would be essential in a classical biological control introduction. Ultimately, the success or failure in the use of egg parasitoids in biological control will likely depend on the research funds invested in it.

8.2 Use of Trichogrammatidae on various crops

Over the world, about 18 species of Trichogrammatidae are being used to control pests on corn, sugar-cane, rice, soybean, cotton, sugar-beet, vegetables, and pine (Hassan 1993). In recent years, an area of over 32 million ha of agriculture and forestry in the world has been treated annually with *Trichogramma* for controlling insect pests (Li 1994).

Some examples of the use of *Trichogramma* against various lepidopterous pests in Canada can be found. Inundative releases were made of: *T. brassicae* against European corn borer in Alberta sweet corn (Yu & Byers 1994); *T. minutum* against spruce budworm in Ontario (Smith et al. 1990; Bai & Smith 1994); *T. pretiosum* against the corn earworm in Nova Scotia (Neil & Specht 1990). However, among these, only Yu & Byers (1994) reported the program as a success, compared with insecticide applications. The host habitat probably influences greatly the amount of parasitism occurring upon a host in several instances (Martin et al. 1981). Finally, many other examples of the use of *Trichogramma* in North America can be found in Olkowski & Zhang (1990).

8.3 Use of Trichogrammatidae on cruciferous crops

A cooperative research project was started in 1980 in the Netherlands and in Germany to look at the possibilities for the biological control of lepidopterous pests in cruciferous crops by mean of inundative releases of *Trichogramma* (Pak & van Lenteren

1984; van der Schaaf et al. 1984; Hassan & Rost 1985; van Heiningen et al. 1985; van Alebeek et al. 1986; van Dijken et al. 1986; Pak et al. 1989; Pak et al. 1988). They started a selection process with a collection of 60 *Trichogramma* strains. Inundative releases of *Trichogramma* were found feasible to control *M. brassicae* in Brussels sprouts, the largest field vegetable in the Netherlands (Pak 1984). Experimental releases of *T. evanescens* and *T. dendrolimi* in Romania against ICW, DBM, and *Mamestra* spp in 1989 gave good results only for *Mamestra* spp (Ciochia 1990).

The situation in European countries is quite different than in North America, for two main reasons. First, more lepidopterous species are present in Europe, as stated in section 2.2.1, and involves at least two species laying egg masses (*P. brassicae* and *M. brassicae*), which affect the parasitism behavior of *Trichogramma* (Glas et al. 1981; van Dijken et al. 1986). In addition, the Noctuid *M. brassicae* is usually accepted by all strains of *Trichogramma*, and it is preferred over both *P. brassicae* and *A. rapae* (Pak et al. 1990). Secondly, the selection for efficient Trichogrammatidae strains in Europe focused on low temperatures efficiency, which is appropriate for their climate, but not necessary for ours.

In Japan, all major pests of cabbage were found to be parasitized to some extent by *Trichogramma* spp (Hirai 1990). A promising program aimed at the release of *T. chilonis* against DBM is currently under development in this country (Nakazawa & Akanuma 1994). *T. evanescens* was introduced from Poland against ICW in Missouri and California in 1965-1967 (Oatman et al. 1968; Parker 1970; USDA 1978). It revealed that *T. evanescens* was a better parasitoid of ICW than the native *T. pretiosum*. Eggs of ICW parasitized by *T. evanescens* were found in plots as far as two miles from release sites. Releases of *Trichogramma* alone controlled the host population when favorable weather prevailed (Parker & Pinnell 1972b).

In Missouri, attempts were made to release both fertile hosts and parasitoids (*T. evanescens* and *C. rubecula*) against the ICW (Parker et al. 1971). Control of ICW by subsequent generations of *T. evanescens* was limited by egg predation in the field (58% to 72% egg predation on average). *T. evanescens* also parasitized eggs of CL, *Chrysopa* spp, and Syrphids. However, detailed laboratory studies were made only after ineffective mass releases against ICW and CL in Missouri (Parker & Pinnell 1974).

Parker & Pinnell (1972a) report effectiveness of the introduced *T. evanescens* and the native *T. pretiosum* on CL and ICW in Missouri. They concluded that *T. pretiosum* was ineffective against both species while *T. evanescens* successfully controlled egg populations of ICW, but was only moderately effective against CL.

Some species of *Trichogramma* are available from commercial insectaries. Most insectaries claim to sell one or more of three species: *T. pretiosum*, *T. platneri*, and *T. minutum*. Of those, only *T. pretiosum* is used to control caterpillar pests in vegetable crops throughout California (Flint 1993). *Trichogramma* must be released in large numbers at peak egg-laying of the pest for maximum effectiveness. Generally, 100 000 to 300 000 wasps/acre must be released to have an effect on pest populations.

9- Selection of species or strains of *Trichogramma*:

9.1 Criteria for selection

There are more than 100 known species of *Trichogramma*, and considerable variation between species exists, especially with respect to host preference, searching capacity and tolerance to weather conditions (Hassan 1994). Prior to a mass production and release program, a sound strategy will include a series of criteria that should be investigated with several candidate species or strains (Hassan 1994). This includes host selection and host acceptability experiments in the laboratory, which are crucial steps in identifying potentially effective species or strains (Pak & van Lenteren 1986). The effectiveness of *Trichogramma* in the field depends largely on its searching behavior (habitat location, host location), host preference (recognition, acceptance, suitability) and tolerance to environmental conditions (Hassan 1990). While searching behavior should be tested in the presence of plants in semi-field or field experiments, host preference, host suitability, as well as tolerance to environmental conditions may be tested successfully in the laboratory (Hassan 1993).

Restricting the discussion only to the first step in the selection of *Trichogramma* species or strains (laboratory experiments), two main aspects have to be considered: the factitious (rearing) host species, and the target host species. The ideal candidate will be one with a high fecundity and longevity on the factitious host, which directly affect production costs. Concerning the target host species, a useful candidate strain should parasitize host eggs of various ages and should not be specific, but parasitize each host species equally well (Pak et al. 1990), and be active for the temperature range to be experienced in field conditions. Space being limited, all aspects of laboratory selection will not be discussed further, but only the aspect I worked on (host age) will be reviewed in more details.

9.2 Host age selection

While a host egg does not vary in size over time, its quality as host will change as the embryo develops (Vinson 1994). During this period the egg's content undergoes extensive morphological and physiological changes that can, in turn, modify the acceptability of the eggs for female parasitoids and the suitability of host eggs for developing parasitoids (Pak 1986; Ruberson & Kring 1993). Usually, host acceptance, successful development of parasitoid larvae, and fecundity of emerging females, which could be taken as an indication of fitness, decrease with host age. Young hosts are accepted more readily than older hosts, and sclerotization of the head capsule of the host embryo often marks the end of host acceptability (Schmidt 1994). Large differences in host age effect between *Trichogramma* species are reported in the literature (Pak 1986). However, conclusions were drawn in most studies from experiments in which the parasitoids were offered only one host age. Nevertheless, hosts of different ages were offered simultaneously in some recent studies (Manweiller 1986; Hintz & Andow 1990; Hutchison et al. 1990; Reznik & Ymarova 1990; van Huis et al. 1991; Li & Henderson 1993; Ruberson & Kring 1993; Takasu & Hirose 1993; Zongo et al. 1993). Generally, young hosts are preferred for oviposition, whereas the size, fitness and number of progenies per host decrease in older host.

9.2.1 Practical considerations

Because timing of a release is one of the most important factors influencing efficacy of *Trichogramma* in the field, host age preference of *Trichogramma* towards a host is fundamental to a release program, and it is a critical factor in selection of an effective species as a biological control agent (Pak & van Lenteren 1986). Also, in order to determine the preferred host species when studying egg parasitoids, it is necessary to determine the preferred development stage of each host species first (van Dijken et al. 1986). In addition, fitness of parasitoids emerging from hosts too young or too old for proper development will be reduced, which may interfere with their efficacy when these individuals are used in the field (Pak 1986). Moreover, host age can have a strong influence on wasp fitness without strongly affecting size (Kazmer & Luck 1995).

9.2.2 Theoretical considerations

Some of the variation in acceptance of hosts of different ages can be explained by optimal foraging theory, which predicts that on encountering a potential host, parasitoids should make 'decisions' as to whether to oviposit or not, how many eggs to deposit, and of which sex, based on potential fitness gain per unit time (Charnov & Skinner 1985; Pak 1986; Waage 1986a). Thus, it is expected that foragers encountering various hosts will show a preference for the most profitable type of host, i.e. the one providing maximal survival and fitness to their progeny (Pyke et al. 1977; Charnov et al. 1981).

A female parasitoid can control how many eggs to lay in available hosts and, in the case of hymenopterous parasitoids, what sex to produce (Waage & Godfray 1985). The decision over sex arises because parasitoids belonging to the order Hymenoptera have an haplodiploid reproduction system, under which males develop from unfertilized, haploid eggs and females from fertilized, diploid eggs. These parasitoid female wasps can thus control the sex of their offspring by choosing whether or not to fertilize an egg (King 1987; Hassell & Godfray 1992). The reproductive strategy of a female includes both progeny and sex allocation (Nadel & Luck 1992), and optimality models have been developed based on the natural selection approach to oviposition decisions (Charnov & Skinner 1985; Waage & Godfray 1985; Waage 1986b; Godfray et al. 1991). With these theories, the mother wasp is expected, when offered a choice, to oviposit preferentially in hosts of relatively high quality, laying more eggs in them and allocating more female progeny.

In conclusion, much more emphasis has been given to practical considerations in the numerous studies on host age selection by Trichogrammatidae (see above). On the other side, the host quality factor usually considered in the development and verification of theoretical models was host size (Waage 1986b; King 1990). However, the integration of the current theory on optimal foraging with host age as a quality attribute, by studying several egg parasitoids species with the same experimental set up, was never attempted.

10. References

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III. SEASONAL OCCURRENCE OF LEPIDOPTEROUS PESTS OF CRUCIFEROUS CROPS IN SOUTHWESTERN QUEBEC IN RELATION TO DEGREE-DAY ACCUMULATIONS

Abstract

Eggs, larvae and adults of *Plutella xylostella* (L.) and *Artogeia rapae* (L.) were monitored on cabbage, broccoli, and Brussels sprouts in 1993-1994 in southwestern Quebec. Using pheromone traps and plant sampling, three to four generations of *P. xylostella* were observed on each plant variety, the first eggs and adults being found during the first week of June. In most cases, adult counts in pheromone traps were not correlated with the number of eggs and larvae on plants. The date at which each generation appeared and their duration varied little between the three *Brassica* varieties. An average of 352.7 degree-days (DD) above 7.3°C were required to complete one generation, but the considerable overlap between generations reduced the usefulness of using DD accumulations to predict *P. xylostella* occurrence. Using visual counts of adults and plant sampling of eggs and larvae, three generations of *A. rapae* were observed on each plant variety, the first eggs being found during the last week of May, two weeks before adults. Butterfly counts were usually correlated with the number of larvae on plant. Plant varieties had no impact on generation occurrence of *A. rapae*, and an average of 319.7 DD above 10.0°C were required to complete one generation.

Key words degree-days, *Artogeia rapae*, *Plutella xylostella*, *Brassica oleracea*, prediction, seasonal ecology, cabbage, broccoli, Brussels sprouts

Introduction

In northeastern North America, cruciferous crops are affected by a complex of three major lepidopterous species: the imported cabbageworm (ICW), *Artogeia rapae* (L.); the diamondback moth (DBM), *Plutella xylostella* (L.); and the cabbage looper, *Trichoplusia ni* (Hübner) (Harcourt 1963). The ICW is usually the dominant pest species, while the relative importance of the other two species is more variable, although they can also reach damaging levels (Harcourt 1955, 1960a, 1963). All three species are multivoltine, but the timing and the number of generations vary between species and between locations (Harcourt 1957, 1962, 1966).

Releases of biological control agents, or applications of insecticides, that are synchronized with early stages of the pests (eggs or young larvae) should substantially increase the efficiency of control measures and reduce the number of interventions. This is especially true when combined with the use of treatment thresholds (Andaloro et al. 1983b). In order to rationalize the use of insecticides for the control of lepidopterous pests of cruciferous crops, treatment thresholds and integrated pest management programs have already been implemented in some parts of northeastern North America (Andaloro et al. 1983a; van Driesche et al. 1990). In Quebec, although sampling procedures and management programs are currently under development, lepidopterous pests control rely mostly on insecticides applied on regular basis (Chagnon et al. 1990).

The use of degree-day (DD) accumulations above a temperature threshold is a method that permits the prediction of insect and plant development (Baskerville & Emin 1969). It can serve to allocate efficiently sampling efforts and control measures around the peak periods of specific instars (Dreistadt & Dahlsten 1990). However, for multivoltine species, the prediction of population peaks may be less reliable because of generation overlaps, particularly in southern countries (Edelson et al. 1988). On the other hand, previous studies in northern regions suggest that the DD accumulation method can reliably predict when the various stages of multivoltine species are dominant (Boivin & Benoit 1987; Boivin 1987; Bracken 1988; Hoffman et al. 1992). Base temperature and thermal requirements are available for the DBM and ICW, but comparisons with field data were done only for the DBM in Ontario (Butts & McEwen 1981; Nealis et al. 1984).

Our objective was to evaluate the reliability of DD accumulation to predict the beginning of generations for the two most important lepidopterous species of cruciferous crops in Quebec: the ICW and the DBM. The cabbage looper occurs sporadically, and can be an important pest (Harcourt 1963), but its low incidence during this two years study prevented analysis. In addition, an attempt was made to determine the influence of different *Brassica oleracea* L. varieties on the timing of the generations, and to investigate the relation between adult counts with eggs and larvae found on plants.

Materials and methods

Monitoring of lepidopterous pests.

Cabbage (*B. oleracea* var. *capitata*), broccoli (*B. oleracea* var. *italica*), and Brussels sprouts (*B. oleracea* var. *gemmifera*) seedlings were transplanted at two (1993) or one (1994, L'Acadie) experimental farms of Agriculture and Agri-Food Canada, located at Ste-Clotilde and at L'Acadie, Quebec. Each plot (29 x 30m) consisted of 30 rows of one variety (90cm between rows) with about 65 plants per row (45cm between plants), and was at least 15m from other plots. To provide attractive plants during all summer, early and late seedlings of cabbage and broccoli were planted in both years. Early plantings were done in mid-May and the plots were sampled until the end of July, while late plantings were done by the end of June and the plots were sampled from the middle of July to the beginning of October. Brussels sprouts were transplanted in mid-May and sampled during all season. Commercial production practices were followed with the exception that no pesticides were applied.

Ten plants were randomly sampled at weekly intervals in each plot, keeping a one meter buffer zone around the plot to avoid an edge effect (Harcourt 1962). The plants were cut down and transported indoor where lepidopterous eggs and larvae were sampled. All larval stage of the DBM were considered together (instars 1 to 4). For the ICW, the development of larvae is longer, and the larval stages considered were small larvae (instars 1 to 3), in order to have a more accurate depiction of generation peaks than when considering all five larval instars. When the plants had more than ten leaves, only every other leaf was considered for population estimates, whereas every fourth leaf was inspected for Brussels sprouts plants with more than 40 leaves.

One pheromone trap (Pherocon 1-C), located at 3m from one of the three plots, was used all season at each location to monitor DBM adults. Pheromone rubber septa (Pherocon® cap) were changed weekly. The traps were checked twice weekly. For the ICW, adults flying over the plots were counted during about five minutes while walking along the rows at the field margin.

Degree-day accumulations.

Threshold temperatures and DD accumulation for the egg to adult period have been documented for the DBM (7,3°C and 293DD) (Butts & McEwen 1981), and the ICW (10°C and 324DD) (Nealis et al. 1984). Unless otherwise stated, we used a common temperature threshold of 10°C for both the ICW and the DBM, as suggested by Pruess (1983). The DD accumulations were calculated, starting April 1, from daily temperatures using the method described by Arnold (1960). Calculations were adjusted with the sine wave method when the minimum temperature was below the threshold (Baskerville & Emin 1969; Allen 1976). Temperature records were obtained from automatic weather stations located nearby the plots.

Data analysis.

For all stages, the beginning of a generation was defined as the day at which 10% of the total number of individuals were captured in each generation, while the generation peak corresponded to 50%. DD accumulations at beginning of generations were compared between the three crucifer varieties using a two-way ANOVA, and between adults, eggs and larvae using a one-way ANOVA. Following differences among treatments, means were submitted to multiple comparisons by a Tukey HSD test. The Student distribution was used to compare observed and predicted values. The relation between adults and eggs or larvae counts was done with a Pearson's correlation analysis (Sokal & Rohlf 1995).

Results and discussion

Seasonal occurrence of the diamondback moth.

Captures of adult DBM in pheromone traps were variable, but it was possible to detect three to four generations, in addition to the overwintering (or migrant) adults in early June (Fig. 3.1). Three to four generations of DBM were detected on each *Brassica* variety, as expressed by eggs and larvae counts on plants, and were best defined on Brussels sprouts (Fig. 3.2, 3.3). However, generations appeared to overlap for all instars (Fig. 3.1, 3.2, 3.3). In warmer localities, four to five generations of DBM were reported in Ontario (Butts & McEwen 1981; Harcourt 1986). Generally, in these and our study, an upward seasonal trend was found in the number of DBM larvae on plants, ending in mid-August (Fig. 3.3).

Degree-days analysis.

By looking at the $DD_{7.3}$ accumulations for DBM egg-laying periods between broccoli, cabbage, and Brussels sprouts (based on eggs occurrence), we found no differences between all three varieties in the first two generations (Table 3.1). The third generation appeared earlier on broccoli than on cabbage and Brussels sprouts. On average, all generations of the DBM appeared to be slightly earlier on broccoli (although not significantly so), whereas the mean duration of generations was the same for all varieties (Table 3.1). Thus, growing three different cruciferous crops in adjacent plots had a small impact on the synchrony of DBM generations, and the three plant varieties were pooled together for further analysis.

It was expected that the use of DD accumulation to monitor the temporal occurrence of the DBM would be more accurate than calendar dates, as it takes into account the impact of thermal requirements on the development of the insect (Baskerville & Emin 1969). However, standard deviations (in days units) were similar between either $DD_{7.3}$, DD_{10} accumulations, or calendar dates (Table 3.2). During the two years of this study, no important thermal variations were experienced between locations and years, which may explain in part the similarities found between the three methods of calculation. By 31 August, the DD_{10} accumulations were of 981.4, 1031.0, and 1008.0 at Ste-Clotilde 1993, and L'Acadie 1993-1994, respectively.

The occurrence of most generations did conform with the predicted DD accumulations (Table 3.2), but the discrepancy between predicted and observed values generally increased from one generation to the next. However, the errors of estimation due to the overlapping generations are likely to increase with the number of successive generations. In addition, the observed generation duration of 352.7 $DD_{7.3}$ was significantly longer than the predicted value of 293 $DD_{7.3}$ found in southern Ontario by Butts & McEwen (1981) in spite of the fact that their value was also calculated with field data. Here again, the fact that the generations are overlapping may have biased our estimate of generation duration, but it is also possible that DBM populations found in more northern regions are different than populations occurring further south. A more accurate method of estimating generations, such as the use of caged insects, would be necessary to clarify the discrepancy between these two studies (Harcourt 1957).

Although the exact threshold for the DBM is 7.3°C, (Butts & McEwen 1981), a common threshold may be more practical in a situation where several pests occur (Pruess 1983). When a threshold of 10°C, which is the estimated developmental threshold for the ICW (Nealis et al. 1984), is used, the variations ranged from ± 4.7 to ± 8.0 days for $DD_{7.3}$, and from ± 5.3 to ± 8.9 days for DD_{10}, which represents an error range of up to two weeks for both thresholds (Table 3.2). The difference between the use of 10°C and 7.3°C thresholds was small enough that the 10°C threshold could be used as well. However, the high variation levels may impede the usefulness of predicting generations for control purpose of the DBM.

Adult monitoring in relation to eggs and larvae.

Both first DBM adult captures and first observations of eggs and larvae on plants occurred at the beginning of June (Fig. 3.1, 3.2). The DD_{10} accumulations at the beginning and the peak of generations for the adult, egg and larval stages are given in Table 3.3. Except for the first generation, it was not always possible to detect adult activity before the occurrence of eggs or larvae on plants, as the occurrence of all stages overlapped with each other (Table 3.3). High variations were observed for all stages in the determination of the beginning and the peak of generations.

The correlations between the captures of adults in traps and the number of eggs and larvae on plants are given in Table 3.4. The results show that the number of adults was rarely correlated with the number of eggs and larvae on plants, and the comparison of adult counts with eggs and larvae sampled a week later (to consider a possible delay in the occurrence of adults and eggs) did not improve the correlation. The few significant correlations were found for the larvae counts during the same week. These results are similar to those of Baker et al. (1982) who found a correlation only 40% of the time. Therefore, while the captures of adults in pheromone traps could indicate the presence of immature stages on plants, as observed in Table 3.3, they would be unreliable to predict the level of infestation (Table 3.4).

Finally, the beginning of generation for any of the stage will overlap with the other stages (Table 3.3), which complicate the task of insect sampling for pest management. Because egg sampling is time consuming and less reliable than sampling larvae, we suggest to rely on adults and larvae counts to estimate populations of DBM on *Brassica oleracea.*

Seasonal occurrence of the imported cabbageworm.

The ICW typically showed three generations during each season with little overlaps (Fig. 3.4, 3.5, 3.6). According to the number of eggs per plant, a fourth generation was sometimes observed on broccoli by the end of September (Fig. 3.5). Although larvae emerged from these fourth generation eggs, they were not able to develop, as shown by the continuous decrease in the number of third generation larvae (Fig. 3.6). A general upward seasonal trend was observed, and the third generation, occurring in late-August, was always the most important one (Fig. 3.6). Similar trends with three generations of ICW were also reported in the nearest studies in Ontario (Harcourt 1962, 1966; Michalowicz 1980).

Degree-days analysis.

The ICW, like the DBM, is found on several cruciferous crops (Renwick & Radke 1983; Huang & Renwick 1993). During our study, no difference was found between the three *Brassica* varieties, both for the beginning and for the duration of each generation (Table 3.5), and the data were pooled for further analysis. Measurements of beginning and peak of generations based on calendar dates and DD accumulations gave good results (Table 3.6). The variations ranged from ± 1.6 to ± 3.9 days for DD_{10} as compared with ± 1.5 to ± 2.7 days for the calendar method. As for the DBM, the use of DD did not increase the precision compared with calendar dates as the thermal variations between locations were low.

The ICW overwinters at the pupal stage in Ontario (Harcourt 1966), and Quebec (Chapter 4). We used the estimated DD_{10} requirements for the pupal stage to calculate the predicted values for the apparition of the first generation, combining the estimated larval + pupal DD_{10} requirements for the subsequent generations (Nealis et al. 1984). The actual occurrence of the generations matched closely the predicted values (Table 3.6), and no statistical differences were found for both occurrence and duration of generations. The mean generation duration of 319.7 DD_{10} was also well within the range of the predicted value of 324 DD_{10}. Finally, although there may have been enough DD accumulation every year for a fourth generation, it did not occur because most pupae of the third generation went into diapause (Chapter 4).

The generations of the ICW were distinct, and it was possible to sample the plants for the eggs with good accuracy, whereas the mimicry of the small larvae (instars 1 to 3) with the foliage render them harder to find. The large larvae (instars 4-5) are easier to detect on plants than the small larvae, and they occurred on average 65.1 ± 47.2 DD_{10} after the small larvae (unpublished data). However, sampling large larvae for treatment purpose would be of limited interest, because of the lower efficiency of treatments against older larvae, as they are likely to be more resistant to treatments, and because the larvae eat 50% more foliage during their last instar than during all their previous stages taken together (Sutherland 1966). A sound strategy should focus on younger stages, before important damages and detectable feces accumulate on the plants.

Adult monitoring in relation to eggs and larvae.

The first ICW eggs were found at the end of May, while adults were only observed more than two weeks later (Fig. 3.4, 3.5). The DD_{10} accumulations at the beginning and the peak of generations for the adult, egg and larval stages are given in Table 3.7. Contrarily to our observations with the DBM, good correlations were observed between adult counts and the eggs and larvae on plants, and these correlations did generally not increase when the adult counts were compared with eggs and larvae sampled a week later (Table 3.8). Thus, the density of adults butterflies would be a good indicator of the level of infestation.

Without a sampling method to evaluate the population densities of adults, it is difficult to obtain sound data. However, some authors have visually estimated butterflies density, apparently without attempting to correlate them with egg or larval densities (Parker 1970; van Driesche 1988). To evaluate the butterfly population over a relatively small area (29 x 30m), took no longer than what was necessary for inspecting and maintaining one pheromone trap (less than 5 min.). This method can be useful because of the short time required to monitor adults, and the good agreement between the number of observed butterflies and the number of eggs or larvae on plants (Tables 3.7 and 3.8). However, at one location (L'Acadie 1994) and during the first generation, where populations were very low, no adult ICW were observed.

One limitation of this method is that the butterflies are active during daytime and mostly when the weather is favorable, i.e. warm, sunny weather and low wind velocity (Dempster 1969). Therefore, no or very few butterflies would be found during rainy or overcast days, even at the peak of an important generation (see Fig. 3.4, L'Acadie 1993 and 1994, late August). If poor weather lasts for a few days, this would result in a delay in plant infestations, but not necessarily in lower infestations, as the female butterfly is able to postpone oviposition (Biever et al. 1972). Consequently, butterflies should be counted only during sunny days.

Finally, the intensity of the infestations might not be always predictable without careful plant sampling, as for the DBM, but the time scheduled for sampling could be reduced and control measures could be improved by the prediction of the occurrence of particular stages in each generation. This might be achieved by monitoring for adults and larvae of the DBM, and by monitoring for adults and eggs of the ICW, through records of DD_{10} accumulations. Especially for the ICW, this method would be useful to reduce the number of biological or insecticide treatments. A positive impact of such a rationale use of insecticides would be to alleviate the deleterious effect of insecticides resistance.

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Table 3.1: Comparisons between beginning of generations (based on 10% of eggs occurrence) of *Plutella xylostella* on three crucifer varieties, according to DD accumulations above 7.3°C.

	DD accumulations (mean ± SD)		
Generation	Broccoli	Cabbage	Brussels sprouts
1	246.8 ± 13.9 a	252.4 ± 15.8 a	306.8 ± 79.5 a
2	544.2 ± 53.7 a	565.6 ± 116.4 a	685.2 ± 126.3 a
3	911.9 ± 51.6 a	979.7 ± 57.7 b	1021.5 ± 40.7 b
4	1348.7 ± 61.5 n.a.	– n.a.	1248.3 ± – n.a.
Mean duration	363.8 ± 98.5 a	363.7 ± 92.5 a	332.1 ± 90.5 a

Means within a row followed by the same letter are not significantly different at P > 0.05 (two-way Anova followed by Tuckey HSD)

Table 3.2: Relationship between DD accumulations, and the observed and predicted dates at the beginning of each generation of *Plutella xylostella* (based on 10% of eggs occurrence), 1993-94.

			DD accumulation (mean ± SD (SD converted in days))				
	Dates (mean ± SD)		Above 7.3°C		Above 10°C		
Generation	Predicted[1]	Observed	Predicted[1]	Observed	Predicted[1]	Observed	n
1	11 June	7 June ± 5.0 ns	293	271.4 ± 52.6 (7.3) ns	189	170.1 ± 44.3 (8.9) ns	8
2	4 July	4 July ± 7.0 ns	586	598.3 ± 111.5 (8.0) ns	415	425.3 ± 94.8 (8.4) ns	9
3	25 July	1 Aug. ± 4.1 *	879	971.0 ± 64.8 (4.7) *	654	723.6 ± 59.0 (5.3) *	9
4	18 Aug.	28 Aug. ± 5.5 *	1172	1315.2 ± 72.4 (6.0) ns	881	996.2 ± 50.4 (5.4) ns	3
5	19 Sept.	--	1465	--	1101	--	-
Mean	25 days	28.2 ± 6.2 *	293	352.7 ± 90.2 **	228	277.7 ± 74.6 **	20

[1] Predicted values taken from Butts and McEwen (1981) estimate of generation time.

Level of significance: * $P < 0.05$; ** $P < 0.01$.

Table 3.3: DD accumulations above 10°C (± SD) and seasonal occurrence of *Plutella xylostella* in southwestern Quebec, 1993-94

Period	Adults	Eggs	Larvae
First generation			
10%	144.3 ± 7.1	170.1 ± 44.3	207.4 ± 34.2
50%	160.5 ± 9.5	201.1 ± 70.2	304.0 ± 28.8
Second generation			
10%	368.5 ± 86.8	425.3 ± 94.8	442.9 ± 61.2
50%	486.8 ± 32.5	521.2 ± 99.5	553.3 ± 52.2
Third generation			
10%	745.4 ± 31.5	723.6 ± 59.0	720.4 ± 79.9
50%	796.3 ± 46.7	779.8 ± 61.3	802.3 ± 69.9
Fourth generation			
10%	1029.6 ± 41.4	996.2 ± 50.4	1016.8 ± 43.8
50%	1062.3 ± 25.2	1024.2 ± 56.8	1061.2 ± 27.1

Table 3.4: Correlations between the number of moths in traps and the number of *Plutella xylostella* eggs and larvae per plant, for the three locations, 1993-94

	Correlation coefficients			
	Eggs		Larvae	
Location	Same week	Week after	Same week	Week after
Ste-Clotilde, 1993				
Broccoli	- 0.28	- 0.35	0.54 *	0.06
Cabbage	0.33	- 0.16	0.67 *	0.13
Br. sprouts	0.43	- 0.01	0.88 *	0.26
L'Acadie, 1993				
Broccoli	0.33	0.17	0.68 *	0.65 *
Cabbage	0.37	0.20	0.46	0.49
Br. sprouts	0.41	0.31	0.37	0.64 *
L'Acadie, 1994				
Broccoli	0.02	- 0.19	0.11	- 0.17
Cabbage	- 0.05	0.02	- 0.05	- 0.24
Br. sprouts	- 0.12	- 0.16	- 0.09	0.01

* Significant correlation, $P < 0.05$

Table 3.5: Comparisons between beginning of generations (based on 10% of eggs occurrence) of *Artogeia rapae* on three crucifer varieties, according to DD accumulations above 10°C.

	DD accumulations (mean ± SD)		
Generation	Broccoli	Cabbage	Brussels sprouts
1	110.6 ± 2.0 a	110.9 ± 10.8 a	108.6 ± 4.3 a
2	422.1 ± 37.2 a	478.2 ± 53.3 a	453.9 ± 43.7 a
3	759.0 ± 36.6 a	762.1 ± 48.1 a	738.3 ± 51.4 a
Mean duration	318.3 ± 26.4 a	325.6 ± 70.6 a	314.9 ± 45.4 a

Means within a row followed by the same letter are not significantly different at $P > 0.05$ (two-way Anova followed by Tukey HSD)

Table 3.6: Relationship between DD accumulations, and the observed and predicted dates at the beginning of each generation of *Artogeia rapae* (based on 10% of eggs occurrence), 1993-94.

	Dates (mean ± SD)		DD accumulation above 10°C (mean ± SD (SD converted in days))		
Generation	Predicted[1]	Observed[2]	Predicted[1]	Observed[2]	n
1	24 May	23 May ± 2.1	107	110.0 ± 6.3 (1.6)	8
2	5 July	7 July ± 2.7	431	451.4 ± 46.1 (3.9)	9
3	4 Aug.	3 Aug. ± 1.5	755	753.1 ± 41.2 (3.7)	9
Mean	36 days	35.8 ± 9.5	324	319.7 ± 49.0	17

[1] Taken from Nealis et al (1984) estimates of larval and pupal development time.

[2] All differences with predicted values were not significant.

Table 3.7: DD accumulations above 10°C (± SD) and seasonal occurrence of *Artogeia rapae* in southwestern Quebec, 1993-94

Period	Adults	Eggs	Larvae
First generation			
10%	233.2 ± 103.2	110.0 ± 6.3	166.6 ± 32.3
50%	273.5 ± 123.2	129.9 ± 15.3	191.2 ± 44.8
Second generation			
10%	502.6 ± 127.2	451.4 ± 46.1	497.5 ± 54.3
50%	588.2 ± 115.3	527.2 ± 28.6	571.8 ± 37.8
Third generation			
10%	825.0 ± 87.0	753.1 ± 41.2	806.9 ± 78.5
50%	900.9 ± 78.8	823.5 ± 55.4	905.5 ± 69.5

Table 3.8: Correlations between the number of flying butterflies and the number of *Artogeia rapae* eggs and larvae per plant, for the three locations, 1993-94

	Correlation coefficients			
	Eggs		Larvae	
Location	Same week	Week after	Same week	Week after
Ste-Clotilde, 1993				
Broccoli	- 0.08	0.02	0.93 *	0.28
Cabbage	0.18	- 0.16	0.60 *	- 0.05
Br. sprouts	0.26	0.31	0.32	0.19
L'Acadie, 1993				
Broccoli	0.25	0.74 *	0.87 *	0.75 *
Cabbage	0.30	0.03	0.97 *	0.55 *
Br. sprouts	0.89 *	0.00	0.95 *	0.45 *
L'Acadie, 1994				
Broccoli	0.90 *	0.54 *	0.50 *	0.92 *
Cabbage	0.98 *	0.61 *	0.50 *	0.96 *
Br. sprouts	0.70 *	0.20	0.67 *	0.80 *

* Significant correlation, $P < 0.05$

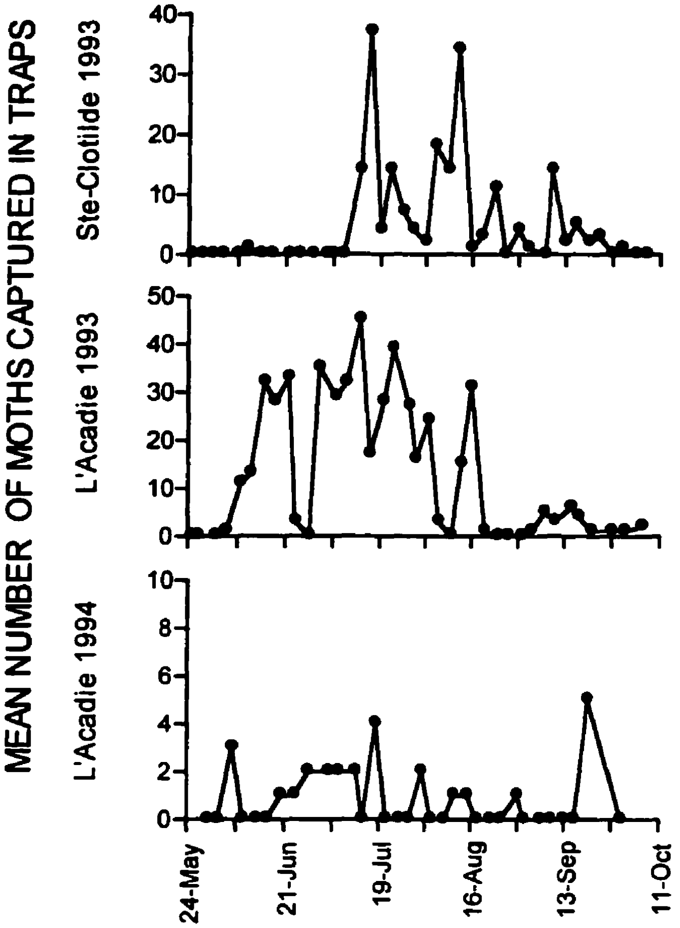

Figure 3.1: Captures of diamondback moth adults in pheromone traps during 1993-1994

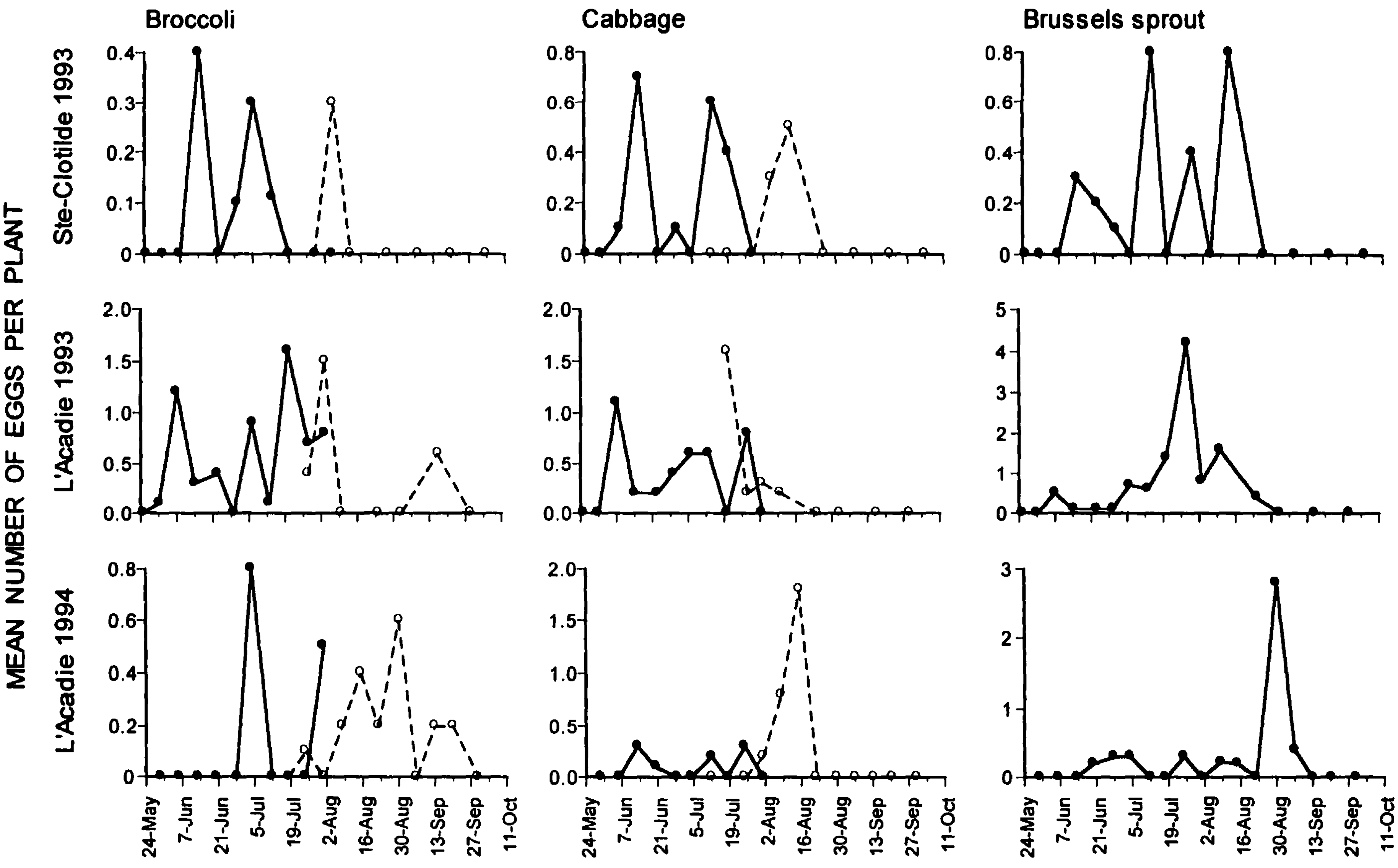

Figure 3.2: Mean number of diamondback moth eggs found on broccoli, cabbage, and Brussels sprouts at Ste-Clotilde during 1993, and at L'Acadie during 1993-1994. Solid lines are early plantings, dotted lines are late plantings.

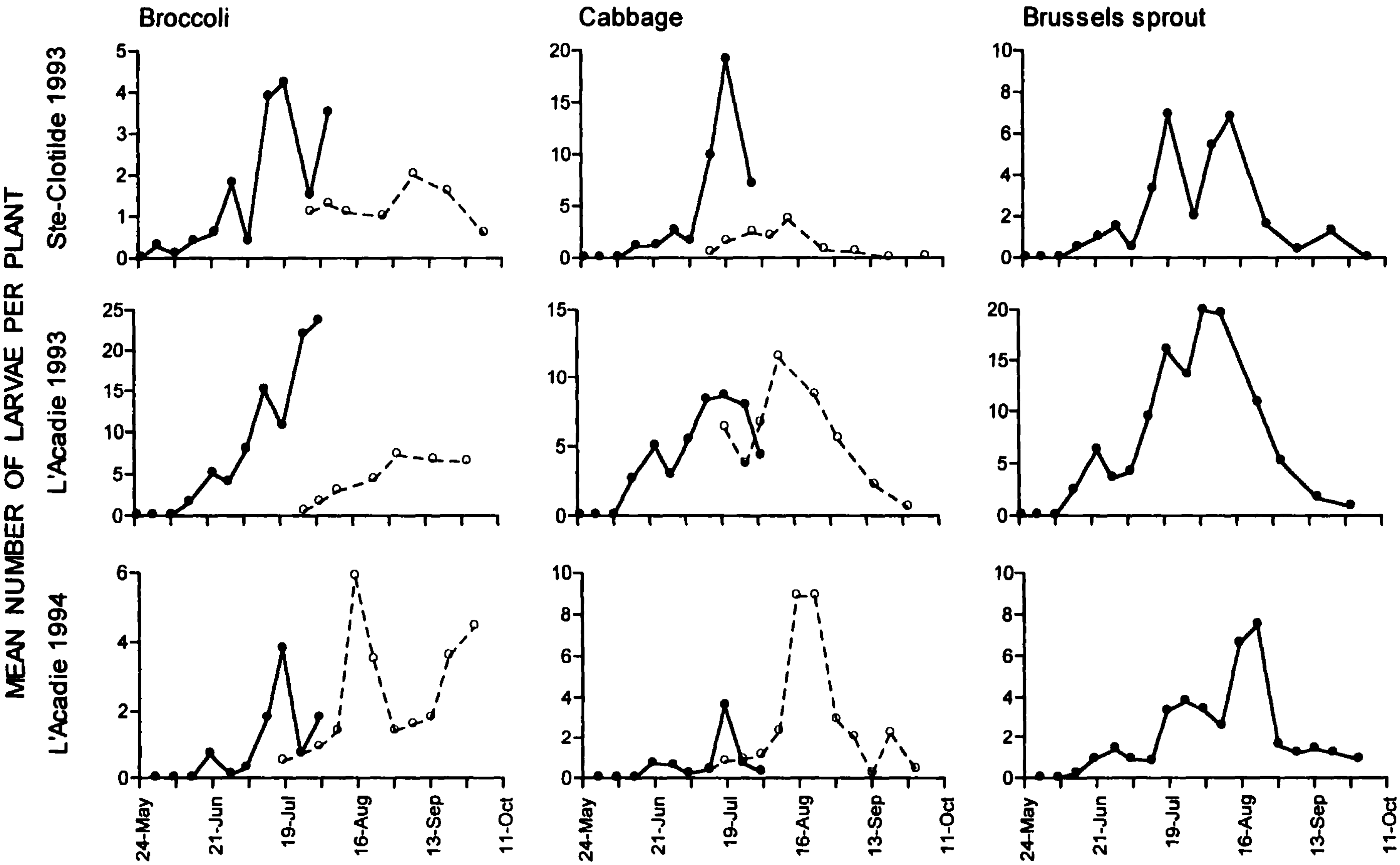

Figure 3.3: Mean number of diamondback moth larvae found on broccoli, cabbage, and Brussels sprouts at Ste-Clotilde during 1993, and at L'Acadie during 1993-1994. Solid lines are early plantings, dotted lines are late plantings.

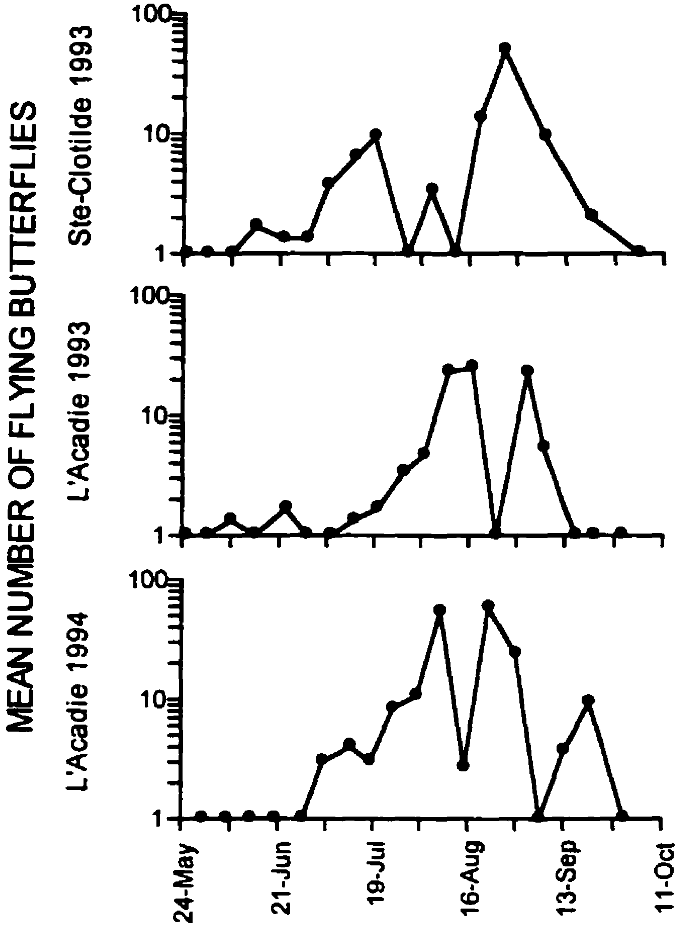

Figure 3.4: Mean number of adult imported cabbageworm counts during 1993-1994

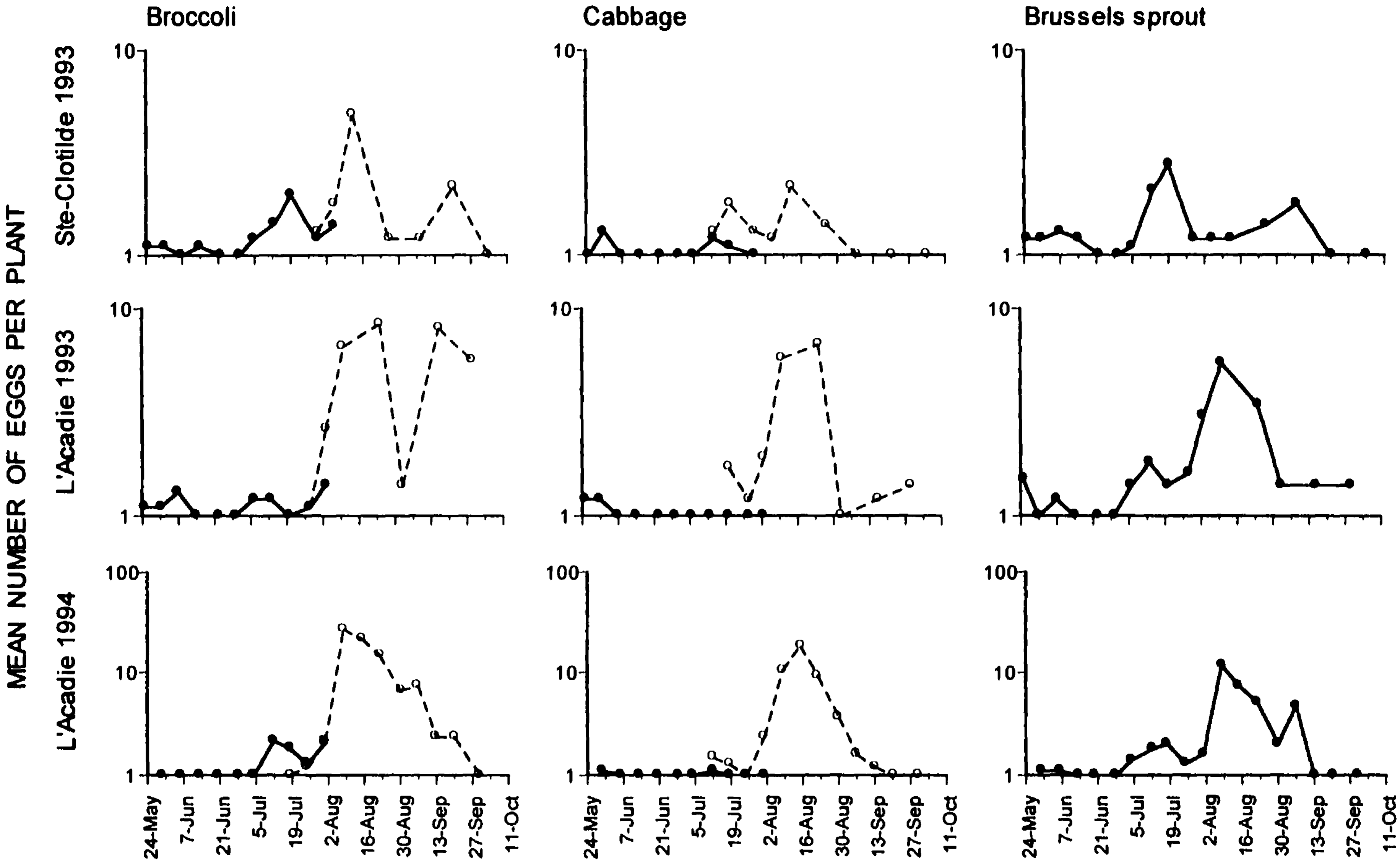

Figure 3.5: Mean number of imported cabbageworm eggs found on broccoli, cabbage, and Brussels sprouts at Ste-Clotilde during 1993, and at L'Acadie during 1993-1994. Solid lines are early plantings, dotted lines are late plantings.

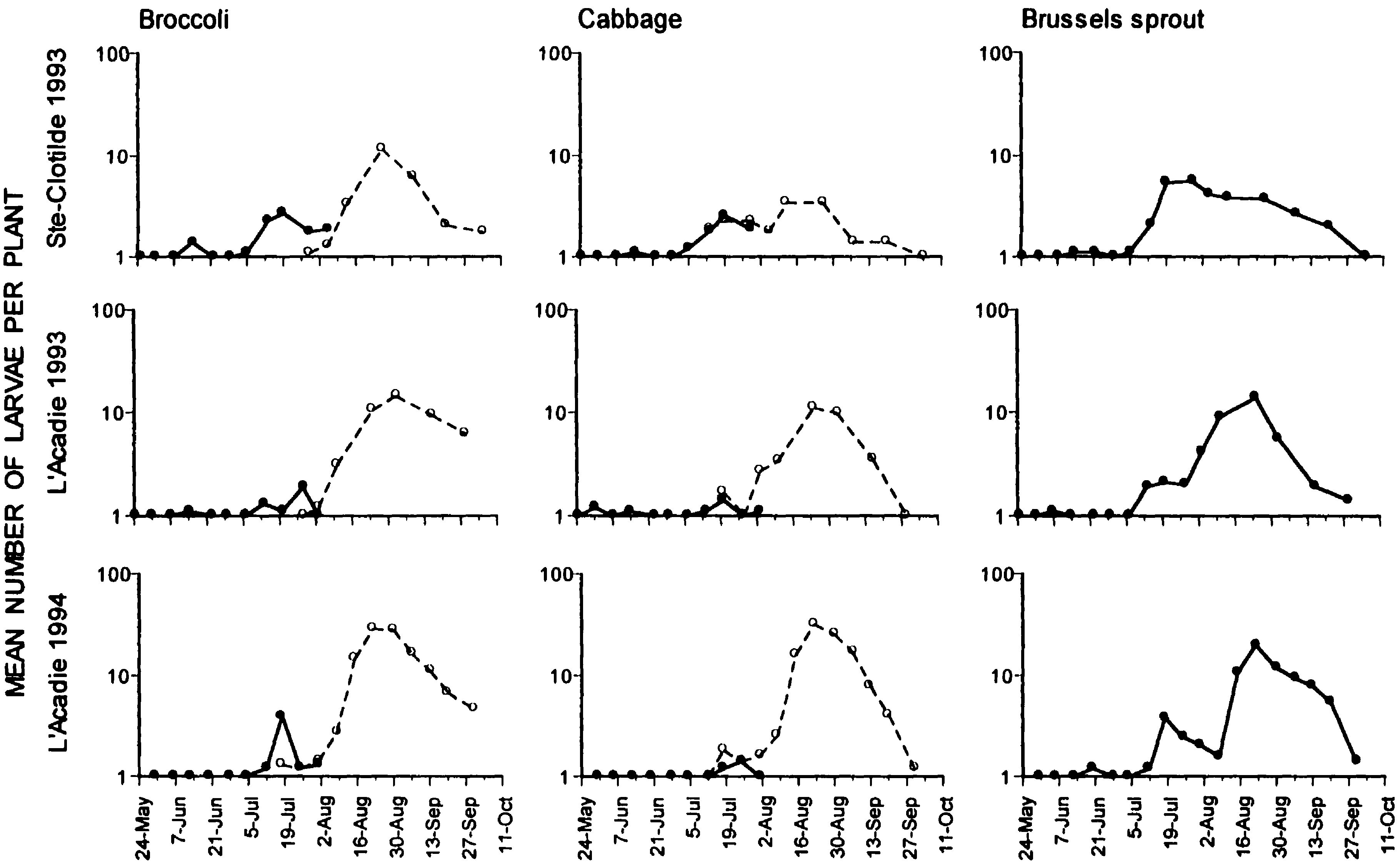

Figure 3.6: Mean number of imported cabbageworm larvae found on broccoli, cabbage, and Brussels sprouts at Ste-Clotilde during 1993, and at L'Acadie during 1993-1994. Solid lines are early plantings, dotted lines are late plantings.

Connecting text

In the preceding chapter, an attempt was made to use the degree-days (DD) accumulation method in order to predict the occurrence of the two most important lepidopterous pests of cruciferous crops, the diamondback moth (DBM) and the imported cabbageworm (ICW). We showed that DBM have four generations each year in southwestern Quebec, while the ICW have three generations, and that the use of DD_{10} accumulation to predict the beginning of each generation was only precise enough for the ICW. By using this method for the ICW, and plant sampling combined with pheromone traps for the DBM and the cabbage looper, it should be possible to synchronize releases of egg parasitoids with the occurrence of the targeted eggs.

However, before any attempts are made to test the efficacy of *Trichogramma* releases in field plots, it is imperative to evaluate the importance of the pest species and to study the complex of natural enemies of the pests we want to control. Such a study serves two purposes: to look for indigenous egg parasitoids that could interfere with released *Trichogramma*, or that can be used for control as well; and to evaluate the importance and composition of the pests and their naturally occurring parasitoid species. An illustrated parasitoid web will serve to synthesize this information in order to discuss the interactions between the parasitoid species and their trophic links in an ecological context. This is the subject of the following chapter.

Chapter submitted to: **Environmental Entomology.**

IV. LEPIDOPTEROUS PESTS OF *BRASSICA* CROPS AND THEIR PARASITOIDS IN SOUTHWESTERN QUEBEC

Abstract

The relative importance of lepidopterous pests of *Brassica* crops and their parasitoids was investigated during a two year study (1993-1994) in southwestern Quebec, on early and late plantings of broccoli and cabbage, and on Brussels sprouts. Seven lepidopterous species were found, with *Plutella xylostella* (L.) and *Artogeia rapae* (L.) being the most common species on early and late plantings, respectively. Infestations of *A. rapae* were more serious on late broccoli plantings, but damaging population levels were nonetheless observed on each *Brassica* variety. A total of fourteen parasitoid and three hyperparasitoid species were reared from the various lepidopterous species (15 Hymenoptera; 2 Diptera). *P. xylostella* and *A. rapae* had the highest parasitism levels and the highest numbers of parasitoid species, with five and six parasitoid species, respectively. Overall, parasitoids accounted for 65% and 43%, and diseases accounted for 22% and 43% of the mortality of *P. xylostella* and *A. rapae*, respectively. The classification of the data into a parasitoid web showed that *Cotesia rubecula* (Marshall), a species not previously reported in Quebec, was the most common parasitoid species. It was able to overwinter successfully under laboratory conditions, as well as its host species, *A. rapae*, and most other parasitoid species. In addition to be the most important larval parasitoid of *A. rapae*, it was the most frequently found with hyperparasitoids (11%). Although several lepidopterous species were found in this system, the most important parasitoids found were monophagous. All hyperparasitoid species were polyphagous and parasitized only the most common parasitoid species. The natural enemies were important only late in the season, and they had not a sufficient impact to control the pests as their effects were restricted to late larval instars and to pupae.

Key words *Artogeia rapae*, *Plutella xylostella*, *Trichoplusia ni*, *Brassica oleracea*, parasitoids, natural enemies, mortality factors, parasitoid web, crucifers

Introduction

In northeastern North America, cruciferous crops are affected by a complex of three lepidopterous species: the imported cabbageworm (ICW), *Artogeia rapae* (L.); the diamondback moth (DBM), *Plutella xylostella* (L.); and the cabbage looper (CL), *Trichoplusia ni* (Hübner) (Pimentel 1961a; Harcourt 1963a; Chagnon et al. 1990). The ICW is usually the dominant pest species, while the relative importance of the other two species is more variable (Harcourt 1955, 1963a). However, the DBM and the CL can also reach high levels (Harcourt et al. 1955; Harcourt 1963a, 1986). All three species have several generations each year, but only the ICW is known to overwinter in northern regions, while the timing and the number of generations vary between species and between locations (Harcourt 1957, 1963a; Renwick & Radke 1983).

Most studies from northern United States have focused on a single pest-crop association (Pimentel 1961a,b; Sutherland 1966; Elsey & Rabb 1970; van Driesche 1988; Biever 1992; Biever et al. 1992), but comprehensive studies were made on the natural control of lepidopterous pests of cabbage in Ontario (Harcourt 1963a, 1966, 1986). However, since then at least one parasitoid species has been introduced in different areas of North America, and the host-parasitoid assemblages may have changed (Wilkinson 1966; Corrigan 1982; Nealis 1985).

No recent studies are available for Quebec, the second most important cruciferous crop production areas in Canada (Richard & Boivin 1994). In the context of establishing a biological control program, our objectives were to evaluate the importance of the lepidopterous species, along with their natural enemies, in a complex of three varieties of *Brassica oleracea* (L.): broccoli, cabbage, and Brussels sprouts. We also investigated the overwintering ability of these species. Finally, we organized the data on the natural mortality of the lepidopterous species into a parasitoid web in order to discuss their relative importance, their host range and interactions between trophic levels (Memmott & Godfray 1994). This information constitute the ecological basis necessary to initiate a biological control program.

Materials and methods

Broccoli (*B. oleracea* var. *italica*), cabbage (*B. oleracea* var. *capitata*), and Brussels sprouts (*B. oleracea* var. *gemmifera*) seedlings were transplanted at two experimental farms of Agriculture and Agri-Food Canada (Ste-Clotilde and L'Acadie, Quebec) in 1993, and at one farm (L'Acadie) in 1994. One 29 x 30m plot was set up for each plant variety, consisting in 30 rows (90cm between rows) with 65 plants per row (45cm between plants), and located 15m from adjacent plots. To provide attractive plants during all summer, early and late seedlings of cabbage and broccoli were planted in adjacent plots during both years. Early plantings were done in mid-May and the plots were sampled until the end of July, while late plantings were done late in June and the plots were sampled from mid-July until October. One or two weeks after their last sampling period, the early plantings were mechanically destroyed. Brussels sprouts were transplanted in mid-May and sampled during all season. Commercial production practices were followed with the exception that no pesticides were applied.

Abundance of lepidopterous pests of crucifers.

Starting two to three weeks after planting, ten plants were randomly sampled at weekly intervals in each plot, keeping a one meter buffer zone around the plot to avoid an edge effect (Harcourt 1962). The plants were placed in plastic bags and brought back to the laboratory where the leaves were carefully examined for all immature stages and pupae of the insects. When the plants had more than ten leaves, only every other leaf was considered for population estimates, whereas every fourth leaf was inspected for Brussels sprouts when it reached more than 40 leaves. To allow for comparison with corresponding early and late plantings of broccoli and cabbage, the Brussels sprouts samples taken during June-July were compared with early plantings of the other two *Brassica* varieties, while the samples taken during August-September were associated with the late plantings.

Natural mortality factors and overwintering.

Eggs, still attached to a piece of leaf, were individually placed in 300µl Beem™ polyethylene embedding capsules, which were in turn placed in a 40ml plastic cup (Solo

Cup no.P125) with a plastic lid (Solo Cup no.PL1) pierced for ventilation. Humidity was maintained in the cup with a 5cm^2 paper towel that was sprayed with distilled water when needed. Individual larvae of DBM were reared on an artificial diet (Shelton et al. 1991), while all other lepidopterous species were reared on fresh cabbage leaves. Pupae of all species were also kept individually, and humidity was maintained as previously mentioned. Incubation conditions were maintained at 24 ± 1°C, with a 16L:8D photoperiod. Eggs of DBM and ICW were kept until larvae or adult parasitoids emergence to evaluate mortality factors. All other stages or species were reared until adulthood or until adult parasitoid emergence.

Parasitism rates were estimated from the most appropriate host instar (the instar between oviposition into the host and emergence of the parasitoid progeny) (van Driesche 1983; van Driesche et al. 1991). For the DBM, known parasitoid species attack principally the first three instars and emerge from the last instar or from the prepupa (Harcourt 1986). Thus, we estimated larval and pupal parasitism from last instar larvae and from pupae, respectively. For the ICW, two Braconidae are known to attack the first two instars and to emerge from the fourth or the fifth instar, whereas Tachinidae attack older larvae and emerge from the host pupae (Harcourt 1966). We estimated parasitism of larvae and pupae from third instar larvae (for Braconidae) and from pupae (for Tachinidae and parasitoids of pupae), respectively. For the other lepidopterous species, the parasitism rates were estimated from the collected instars.

In October, pupae that did not hatch after three to four weeks were considered in diapause and were placed at 10 ± 1°C without light for one week, and then at 4 ± 1°C in complete darkness for winter. After five months, they were brought back at the previous rearing conditions for up to two months to evaluate pre-diapause and diapause mortality.

Relative importance of lepidopterous and parasitoid species.

We used pooled data to generate a quantitative parasitoid source web (Memmott & Godfray 1994). The observed parasitism rates were transformed in¨to comparable units to account for the mortality occurring during previous instars. For example, a 50% mortality of the pupal stage would account for only 25% of the total mortality if 50% of the larvae were previously found to be parasitized. The resulting web represents the general trends that were observed on crucifers during this study, and highlights the relative importance of the lepidopterous and parasitoids species.

Data analysis.

Data on abundance of the lepidopterous species were analyzed using a two-way ANOVA (the two criteria being the plant varieties and the sampling weeks) followed by Tukey HSD multiple comparisons (Sokal & Rohlf 1995). A logarithm transformation, $\log_{10}(x+1)$, was performed before the analysis to make the variance independent of the mean (Sokal & Rohlf 1995). Parasitism rates (proportions) were analyzed with log-linear models (*G*-test of independence) and William's correction for continuity, and if there were significant differences, it was followed by the STP method at $P < 0.05$ (Sokal & Rohlf 1995).

Results and Discussion

Abundance of lepidopterous pests of crucifers.

Diamondback moth:

The DBM completes four generations each year in southwestern Quebec, the first two being completed mostly during early plantings and the third and fourth ones during late plantings. Very low numbers of DBM eggs were found at all locations, on both early and late plantings, and the number of eggs found were not significantly different for any of the three *Brassica* varieties (Fig. 4.1). On average, DBM egg counts rarely exceeded 0.5 per plant, except at L'Acadie during 1993.

DBM larvae were found throughout the season, with population levels varying between the three *Brassica* varieties, and with means (over the period of both early or late plantings) of up to 10 larvae per plant during 1993 at L'Acadie (Fig. 4.1). Numbers of DBM larvae varied occasionally between the three plant varieties, but no general trends were observed.

The differences in density of DBM pupae between the three plant varieties were similar, most of the time, to the differences previously observed for the larvae (Fig. 4.1), suggesting that the impact of natural mortality factors between the larval and pupal stages was the same on the three varieties. However, as opposed to the number of larvae, the number of pupae found on broccoli was often lower than on cabbage and Brussels sprouts. It was particularly the case for early plantings at L'Acadie (1993) where the larvae were previously the most numerous on that variety (Fig. 4.1). This may indicate a higher mortality on broccoli (see below), or emigration of the mature larvae for other pupation sites, which is unlikely as the larvae are not reported to behave in such a way (Harcourt 1986).

As no regular trends were observed, no preferrence could be inferred. Similarly, Harcourt (1986) stated that the DBM was found equally between these varieties, but new lines of cabbage seemed to have some resistance to this pest in the United States (Talekar & Shelton 1993).

Imported cabbageworm:

ICW showed more consistent trends than DBM (Fig. 4.2). This species has three generations each year in southwestern Quebec (Chapter 3), but the population levels observed during the first half of the season are usually below 1.5 larvae per plant, often being outnumbered on early plantings by the DBM (Fig. 4.1 and 4.2). However, during its third generation (on late plantings), a 10 to 40 fold increase in the number of ICW larvae per plant, from the early to the late plantings, was not uncommon (Fig. 4.2, compare numbers on left and right scales).

It appeared that the ICW, during the first half of the season, preferred significantly Brussels sprouts and broccoli over early plantings of cabbage, as expressed by the number of eggs on plants (Fig. 4.2). However, during the second half of the season, the late planting of broccoli was strongly preferred for oviposition over late cabbage and Brussels sprouts. Indeed, at least twice the number of eggs were found on broccoli than on the other two varieties (Fig. 4.2).

This preference for broccoli over other cruciferous crops was also found in other studies (Pimentel 1961c; Ives 1978; Jones & Ives 1979; Latheef & Irwin 1979; Stoner 1990, 1992). The reasons why broccoli is more attractive to ICW females are unknown, but the ovipositing butterfly is guided by contact kairomones (Renwick & Radke 1983). The leaves of broccoli are thinner and their glossy appearance is different than the other two varieties. Broccoli metabolism also differs from those of cabbage and Brussels sprouts: it concentrates its energy on leaves and flowers production, while the other two varieties focus on storing resources (sprouts, cabbage head), and do not produce flowers during the first growing season. This suggests that larger leaf surfaces and important growing activities might result in different concentrations of compounds detectable by the ICW females.

The highest numbers of ICW larvae were also found on Brussels sprouts early in the season, and on broccoli later in the season (Fig. 4.2). However, the number of larvae on Brussels sprouts often reached levels similar to the ones on late broccoli plantings. The average number of larvae per plant remained below two during the first half of the summer, so that early plantings of broccoli and cabbage were practically not affected by this species and would have required few or no control treatment at all. However, the population levels found on the second plantings were much more important, with overall averages of up to 20 larvae per plant, except for the populations of larvae at Ste-Clotilde did not reach high levels on late plantings (Fig. 4.2). If we assume that the migration rate of butterflies into the fields was similar for both locations in 1993 (Ste-Clotilde and L'Acadie), this result suggests that high mortality rates early in the season prevented the buildup of the ICW population at Ste-Clotilde (see below).

Finally, the number of pupae often varied between the three crucifer varieties in a different way than the number of larvae (Fig. 4.2). Although this can result from different mortality rates of the larval stage between the three varieties, the mature larvae are also known to migrate off the host plant to pupate, especially when populations are high (Harcourt 1963a, 1966).

Other lepidopterous species:

The ICW and the DBM were the most abundant lepidopterous species, but low populations of other species were also found during this study, the most important one being the CL. Although populations of the CL can build up to high levels (Harcourt 1960a), this species never exceeded 2.0 larvae/plant in this study. Most CL larvae were collected in August and September, and the number of larvae usually peaked at the same time as the ICW.

Four other lepidopterous species were found, with rarely more than one specimen on a single plant. Three of these species were Noctuids that are not restricted to crucifers: the clover cutworm, *Discestra trifolii* (Hufnagel), the spotted cutworm, *Xestia c-nigrum* (L.), and the zebra caterpillar, *Melanchra picta* (Harris). Despite their low numbers, they can locally damage cruciferous crops, especially young seedlings which are cut down near the soil level. In addition, a large Arctiidae, the saltmarsh caterpillar, *Estigmene acrea* (Drury), was sometimes found. Altogether, these four species were not as important as CL, but their occurrence was not restricted to the end of the season (unpublished data). The species composition was similar to the one reported by Harcourt (1963a) in Ontario, who found five species of minor importance.

Natural mortality factors.

Diamondback moth:

No egg parasitoid was found, whereas the larvae of the DBM were attacked by a parasitoid complex dominated by the Ichneumonid *Diadegma insulare* (Cresson) and the small Braconid *Microplitis plutellae* (Muesebeck). All the DBM parasitoids that we found were solitary species, and the most important ones were the same as observed elsewhere in North America (Harcourt 1960b, 1986; Talekar & Shelton 1993). However, another Braconid, *Cotesia* sp, and an Ichneumonid wasp, *Stictopisthus bilineatus* (Thompson) were identified (Table 4.1). Viral and fungal infections were found at low incidence, while naturally occurring *Bacillus thuringiensis* (Berliner) was also isolated from DBM larvae during another study covering nearby agricultural regions (J.C. Côté, personal communication).

An average of 70% of the DBM larvae were killed by natural enemies and diseases (Table 4.2). Usually more than 50% of the larvae were parasitized by *M. plutellae* and *D. insulare* in both early and late plantings (Table 4.2). *D. insulare* was usually the most important parasitoid with a maximum of 77% parasitism on late plantings, whereas the maximum observed for *M. plutellae* was 43% (Table 4.2). Higher parasitism rates of *D. insulare* over *M. plutellae* were also observed in previous studies in Ontario (Harcourt 1960b, 1986). However, at L'Acadie in 1993, where the host populations were high (Fig. 4.1), *M. plutellae* was the most important parasitoid species (Table 4.2).

The total parasitism rates of DBM larvae found on Brussels sprouts were often significantly lower than on early broccoli and cabbage (Table 4.2). In contrast, later in the season, parasitism usually increased on Brussels sprouts to reach the same or higher levels than on late broccoli and cabbage (Table 4.2). The low numbers of DBM pupae constantly found on broccoli (Fig. 4.1) could not be explained by a higher mortality due to parasitoids or diseases during the larval stages. However, the mobility of some generalist predators of DBM on *Brassica* leaves can also be influenced by the plant variety (Eigenbrode et al. 1995). If the surface of broccoli leaves improves the mobility of predatory insects, as compared with cabbage and Brussels sprouts, this mortality factor may had an impact on the number of surviving DBM larvae, but this factor was not measured.

Parasitism by the other two larval parasitoids, *S. bilineatus* and *Cotesia* sp, occurred mostly at the end of summer and never accounted for more than 3% and 5% of the mortality, respectively. In addition, *S. bilineatus* was found only during 1993 at L'Acadie. The only other important mortality factors of the DBM larvae were diseases. They occurred regularly, but with no particular trend, and rarely killed more than 20% of the larvae (Table 4.2). Although not negligible in this study, diseases-induced mortality of the DBM has rarely been reported in the literature (Oatman & Platner 1969; Harcourt 1986; Annamalai et al. 1988; Talekar & Shelton 1993; Pell & Wilding 1994).

The only pupal parasitoid of the DBM, *Diadromus subtilicornis* (Gravenhorst) (Ichneumonidae), accounted for up to 24% mortality of this stage (Table 4.3). The parasitism of pupae did not show any particular seasonal trend and was relatively low, especially when compared with the mortality of larvae. In contrast, up to 35% of the pupae failed to develop probably due to diseases or parasitoid development failures. There was generally no difference in mortality of pupae between *Brassica* varieties (Table 4.3).

Imported cabbageworm:

Parasitism of ICW eggs, the most important lepidopterous species, was almost non-existent, as we found only one egg parasitized by a *Trichogramma* species (in 1993 at L'Acadie). In contrast, larvae were parasitized by a complex of four parasitoid species: two Braconids (the gregarious *Cotesia glomerata* (Muesebeck) and the more recently introduced solitary *C. rubecula* (Marsh.)) and two Tachinids (*Phryxe vulgaris* (Fallén) and *Compsilura concinnata* (Meigen)). The pupae were regularly parasitized by a gregarious Pteromalid, *Pteromalus puparum* (L.) (Table 4.1). The parasitoid species composition was similar to what is reported in other North American studies (Blunk 1957; Harcourt 1966; Sutherland 1966; Wilkinson 1966; Beirne 1971) and in Europe (Richards 1940; Dempster 1969). However, *C. rubecula* was not reported in older studies, as its establishment in northeastern United States and in Ontario is recent (Corrigan 1982; Nealis 1985).

Both ICW larval population density and parasitism level were low early in the season, whereas parasitism levels of 23% and higher were observed on late plantings (Table 4.4). However, no consistent patterns were detected between the *Brassica* varieties, despite the preference of the ICW for broccoli (Table 4.4; Fig. 4.2). *C. glomerata* parasitized no more than 20% of the ICW larvae while *C. rubecula* parasitism rates reached up to 63% on late plantings (Table 4.4), at a time when the ICW population levels were the highest (Fig. 4.2). Overall, 25% to 36% of the ICW larvae were parasitized by these two species (Table 4.4).

A substantial proportion of larvae (up to 69%) were killed by pathogenic infections, without particular seasonal trends (Table 4.4). Although the infecting agents were not identified, the dead larvae and pupae showed symptoms of viral (liquefaction) or fungal (mycelium) diseases, the virus being predominant. In addition, the bacterium *B. thuringiensis* was isolated from larvae sampled at both locations during 1993 (J.C. Côté, personal communication). Supporting our observations, Harcourt (1966) stated that a granulosis virus disease was the key mortality factor of the ICW in Ontario. Of particular interest is the high incidence of diseases, early in the season at Ste-Clotilde in 1993, that may have prevented the buildup of the subsequent generations (Table 4.4; Fig. 4.2). Finally, the absence of regular differences in the level of mortality between the *Brassica* varieties suggests that the discrepancy between the numbers of larvae and pupae on late plantings, stated in the previous section, was principally the result of migration of mature larvae to other pupation sites because of high larvae densities on plants (Harcourt 1963a).

The maximum parasitism level of ICW pupae was 24% and 31% for *P. vulgaris* and *P. puparum*, respectively (Table 4.5). Parasitism by these two species occurred more regularly when the host population was high (on late plantings), but no differences were found between *Brassica* varieties (Table 4.5). Diseases accounted for most of the pupal mortality, with no consistent trends between the varieties, reaching a maximum of 62% on Brussels sprouts (Table 4.5).

Other lepidopterous species:

Parasitism rates of other lepidopterous species found on crucifers stayed at low levels. Moreover, few of the frequently reported parasitoids of the CL were found (Harcourt 1963a; Sutherland 1966; Beirne 1971; Chamberlin & Kok 1986), the only important species being the Eulophid *Copidosoma floridanum* (Ashmead), an egg-larval parasitoid (8 parasitized CL larvae on a total of 120 specimens) (Table 4.1). This polyembrionic wasp lays its eggs in CL eggs and hundreds of adults emerge from one host, but only after the prepupal host stage, leading to an increase in foliage consumption by the host larva (Hunter & Stoner 1975). If the populations of the CL become more important, this parasitoid would probably be the only potential competitor against other control agents such as egg parasitoids. Other parasitoid species found are presumably generalists that attack large larvae such as Noctuids (Table 4.1). A virus-like disease killed a substantial portion of the CL population (21%), but this factor is expected to be important only at high host densities (Harcourt 1960a, 1963a).

Concerning the other four minor lepidopterous species, only *Meteorus* sp and *Aphanistes* sp were occasionally found in *X. c-nigrum*, and *Enicospilus* sp in *D. trifolii*, whereas many larvae apparently died of diseases. The numbers of diseased larvae on the total of sampled larvae were: *D. trifolii* 26/36, *X. c-nigrum* 28/55, *M. picta* 38/55, and *E. acrea* 9/29. These high levels of infection may be the result of stress during the rearing process (although the DBM, the ICW and the CL were not affected), or that these generalist species were unable to develop to adulthood because they are not well adapted to substances found in cruciferous crops (Erickson & Feeny 1974; Blau et al. 1978).

Overwintering.

We found no evidence of overwintering of DBM under laboratory conditions. However, three of its parasitoids survived under the same conditions (Table 4.6). The larvae of DBM found early in the spring are believed to originate from migrating adults (Harcourt 1960b; Putman 1973; Smith & Sears 1982), while some of their parasitoids can probably overwinter. It is possible that those parasitoid species maintain themselves on other hosts, but the common *M. plutellae* is believed to be specific to the DBM in Canada (Harcourt 1986; Putman 1973). Nevertheless, the first DBM generation was regularly observed during the same period each year (Chapter 3), suggesting that this moth could overwinter at the adult stage, possibly in warmer localities. The overwintering ability of *M. plutellae* did not seem to give this species an advantage over *D. insulare* (that did not survive through simulated winter) because the latter was usually more important than *M. plutellae* on early plantings (Table 4.2).

The ICW and three of its parasitoids overwintered successfully under laboratory conditions (Table 4.6). In the case of *C. rubecula*, this aspect further supports its establishment in southwestern Quebec. In contrast, no diapausing cocoon of the gregarious *C. glomerata* was found. The overwintering ability of *C. rubecula* is probably an important asset for its establishment in northern regions. Conversely, its early diapause was also reported to be a limiting factor in southern countries (Biever 1992).

Relative importance of lepidopterous and parasitoid species.

The parasitoid webs approach described by Memmott & Godfray (1994) was used to discuss the host-parasitoid community as a whole, and the possible interactions between species. A quantitative parasitoid source web was built from our estimates of lepidopterous populations and mortality factors, which were discussed separately in the previous sections for eggs, larvae and pupae. By definition, a parasitoid web is, compared with a conventional community food web, restricted to phytophagous species and their parasitoids. It is thus a subset of the former. In addition, in a quantitative web, the trophic links are reported along with their weighted importance, as compared with a connectance web which shows only the trophic links. Finally, the distinction between a source web and a sink web is that the former begins with a herbivore and includes all higher trophic levels, while the latter is centered around a predator (or parasitoid) and includes all lower trophic levels related to it (Memmott & Godfray 1994).

Figure 4.3 displays at a glance the lepidopterous pest complex and their parasitoids in an agricultural cruciferous crops system (the complete parasitoid species identifications are listed in Table 4.1). The insect parasitoids and hyperparasitoids were placed above their lepidopterous hosts in Fig. 4.3 to illustrate their trophic relationships.

Among the parasitoid species, the Tachinid flies (#18-19) was the only group of natural enemies shared by more than one lepidopterous species, and they were not attacked by hyperparasitoids. Most of the primary parasitoids were Hymenoptera that attacked only one host species on crucifers, whereas hyperparasitoids were more generalist (Fig. 4.3). In fact, hyperparasitoids were reared only from the most numerous parasitoid species. Thus, variations in population density of one of the lepidopterous species will likely not affect the parasitism of the other ones (except for Tachinid flies), but may affect the hyperparasitism rates, as their parasitoid hosts become more or less abundant. However, most *B. galactopus* (#17) were recovered from *Cotesia* spp (#1-2) although two parasitoids of the DBM (#3, #6) were also abundant (Fig. 4.3).

Of the hyperparasitoid species identified, only *B. galactopus* is commonly reported in the literature as an hyperparasitoid of the two Braconids *C. glomerata* and *C. rubecula* (Parker 1970; Puttler et al. 1970). High hyperparasitism rates have been found to interfere with the introduction of *C. rubecula* in southern regions (Puttler et al. 1970), but in our study hyperparasitism of this parasitoid was low (11%) and should not be a limiting factor. Finally, contrarily to most primary parasitoids, hyperparasitoids are generally not restricted to a single host (Table 4.1, Fig. 4.3).

Diseases, that could be considered functionally as parasitoids (Eggleton & Gaston 1990), have been included in the parasitoid web but were considered as a single class and placed at the bottom of the web (Fig. 4.3). As some diseases affecting the lepidopterous species are relatively specific (Kelleher & Hulme 1984; Jaques & Harcourt 1971), they were kept separated for each host species. However, parasitoid species may interact with the spread of a disease (Levin et al. 1981, 1983), making these two factors not completely unrelated. In addition, a proportion of the larvae may have been infected during our manipulations. Therefore, the relative importance of the parasitoid species should be considered as minimum values, and the diseases as maximum values.

As shown in Fig. 4.3, a high proportion of the ICW population (43%) failed to complete their development because of diseases, while the same proportion were killed by parasitoids. The parasitoid complex of the ICW was dominated by *C. rubecula* (27%). For the DBM, diseases were responsible for 22% of mortality, whereas the parasitoids accounted for 65%, mostly by *D. insulare* (34%) and *M. plutellae* (25%). Concerning the CL, only 21% and 16% of all the specimens found were killed by diseases or parasitoids, respectively. Finally, almost all rare lepidopterous species that were unable to complete their development on crucifers died of diseases (31% to 69%), while the parasitoids found were generalist species (Table 4.1).

The use of a parasitoid web to illustrate the mortality factors of insects overlooks some other potentially important factors such as predators and weather. However, the predators found on crucifers were generalist or primarily aphidophagous species, such as Coccinellidae and Chrysopidae, that would only secondarily attack lepidopterous species (Sutherland 1966; Elsey & Rabb 1970). The weather, such as heavy rainfalls, has sometimes been shown to affect pest populations (Harcourt 1963b, 1966). Although biological or physical factors other than parasitoids and diseases may reduce pest populations, the dominant parasitoid species showed in the web would probably remain the same ones, unless pesticides are used and kill a portion of the parasitoid population.

We observed, as in previous studies made in North America, that natural control of lepidopterous pests by their parasitoids was insufficient for commercial control (Harcourt 1963b, 1966; Hamilton 1979). Blunk (1957) suggested that the absence of the European larval parasitoid, *C. rubecula*, may explain why the ICW populations were much higher in North America than in Europe. However, now that *C. rubecula* is established, and is indeed the dominant parasitoid species, the ICW populations are still not controlled by their natural enemies until the last generation. By then, the populations of larvae have already reached damaging levels. The extent to which the mortality of the last ICW generation prevents higher infestations during spring by reducing the overwintering population is not known, but we suspect this impact to be unimportant because of immigration and of the high reproductive potential of the ICW (Jones & Ives 1979; Root & Kareiva 1984).

In conclusion, none of the three *Brassica* varieties showed regular intrinsic or extrinsic resistance to infestation by lepidopterous pests. A simple explanation for the ineffective natural control is that the parasitoid induced mortality comes too late in the season, and too late in the developmental stage of the lepidopterous species. A more effective biological control would be achieved with higher parasitism rates early in the season, concentrating on early life stages of the pests (such as eggs or young larvae). This approach would lead to a control of the lepidopterous pests before the damaging feeding action of maturing larvae. During this study, we showed that the mortality of such young stages is almost non-existent, which validate control efforts that concentrate on these stages.

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Table 4.1: Parasitoids and hyperparasitoids reared from lepidopterous hosts and from their parasitoids collected on *Brassica* crops in southwestern Quebec, during 1993-1994

No.[a]	Parasite	Host stage(s) affected	Host(s) [b]
	Hymenoptera:		
	Braconidae		
1	*Cotesia glomerata* (Muesebeck)	Larva	*A. rapae*
2	*Cotesia rubecula* (Marshall)	Larva	*A. rapae*
3	*Microplitis plutellae* (Muesebeck)	Larva	*P. xylostella*
4	*Cotesia* sp.	Larva	*P. xylostella*
5	*Meteorus* sp.	Larva	*X. c-nigrum*
	Ichneumonidae		
6	*Diadegma insulare* (Cresson)	Larva	*P. xylostella*
7	*Diadromus subtilicornis* (Gravenhorst)	Pupa	*P. xylostella*
8	*Stictopisthus bilineatus* (Thompson)	Larva	*P. xylostella*
9	*Gelis* sp.	Pupa	2 - 3 - 6
10	*Enicospilus* sp.	Pupa	*D. trifolii*
11	*Stenobarichneumon* sp.	Pupa	*T. ni*
12	*Aphanistes* sp.	Pupa	*X. c-nigrum*
	Trichogrammatidae		
13	*Trichogramma* sp.	Egg	*A. rapae*
	Pteromalidae		
14	*Pteromalus puparum* (L.)	Pupa	*A. rapae*
15	*Trichomalopsis* sp.	Pupa	3 - 6
	Encyrtidae		
16	*Copidosoma floridanum* (Ashmead)	Egg-larva	*T. ni*
	Eulophidae		
17	*Baryscapus galactopus* (Ratzeburg)	Larva-pupa	1 - 2 - 6
	Diptera:		
	Tachinidae		
18	*Phryxe vulgaris* (Fallén)	Larva-pupa	*A. rapae*
19	*Compsilura concinnata* (Meigen)	Larva-pupa	*A. rapae* - *T. ni*

[a] Numbers used in Fig. 3 for species identification.

[b] Species numbers are used to identify hosts of hyperparasitoids.

Table 4.2: Major mortality factors (%) of *Plutella xylostella* larvae on broccoli, cabbage, and Brussels sprouts during 1993-1994

	Early crops			Late crops			
	Broc.	Cab.	B.spr.	Broc.	Cab.	B.spr.	Total
Ste-Clotilde, 1993							
Number of hosts[a]	67	143	58	38	37	70	413
M. plutellae, %	12a	2b	4ab	13	11	17	8
D. insulare, %	42ab	51a	24b	40b	43b	77a	48
Total parasitism, %	54a	53a	28b	53b	54b	94a	57
Diseases, %	19	15	12	5	8	0	11
Total mortality, %	73a	68a	40b	58b	62b	94a	68
L'Acadie, 1993							
Number of hosts[a]	239	180	201	95	140	243	1098
M. plutellae, %	36a	29ab	19b	41	36	43	34
D. insulare, %	24	22	22	25	29	31	26
Total parasitism, %	60a	52ab	41b	66	64	75	60
Diseases, %	9	17	12	11	14	12	10
Total mortality, %	69a	69a	53b	77b	78ab	87a	70
L'Acadie, 1994							
Number of hosts[a]	42	32	77	95	145	102	493
M. plutellae, %	21	13	21	28a	18a	4b	17
D. insulare, %	38	50	29	30b	44ab	53a	41
Total parasitism, %	60	63	49	58	62	57	58
Diseases, %	5	6	13	21	14	10	13
Total mortality, %	65	69	62	79	76	67	71

Percentages within a row and for the same cropping period, followed by the same letter are not significantly different: *G* test followed by STP procedures, $P > 0.05$.

[a] Total number of fourth instars collected.

Table 4.3: Major mortality factors (%) of *Plutella xylostella* pupae on broccoli, cabbage, and Brussels sprouts during 1993-1994

	Early crops			Late crops			
	Broc.	Cab.	B.spr.	Broc.	Cab.	B.spr.	Total
Ste-Clotilde, 1993							
Number of hosts[a]	7	82	24	12	36	28	189
D. subtilicornis, %	0	9	0	17	11	7	8
Diseases, %	0	23	21	25	14	14	19
Total mortality, %	0	32	21	42	24	21	27
L'Acadie, 1993							
Number of hosts[a]	84	213	129	26	73	80	605
D. subtilicornis, %	24a	21a	9b	8	14	23	17
Diseases, %	12a	31b	17a	8	14	23	21
Total mortality, %	36ab	52a	26b	16b	28ab	46a	38
L'Acadie, 1994							
Number of hosts[a]	17	15	67	17	87	59	262
D. subtilicornis, %	6	7	12	0	8	3	7
Diseases, %	35	20	24	29	23	20	24
Total mortality, %	41	27	36	29	31	23	31

Percentages within a row and for the same cropping period, followed by the same letter are not significantly different: *G* test followed by STP procedures, $P > 0.05$.

[a] Total number of pupae collected.

Table 4.4: Major mortality factors (%) of *A. rapae* larvae on broccoli, cabbage, and Brussels sprouts during 1993-1994

	Early crops			Late crops			
	Broc.	Cab.	B.spr.	Broc.	Cab.	B.spr.	Total
Ste-Clotilde, 1993							
Number of hosts[a]	24	13	35	106	43	31	252
C. glomerata, %	0	0	0	7	2	6	4
C. rubecula, %	8	0	6	28	28	19	21
Total parasitism, %	8	0	6	35	30	26	25
Diseases, %	63	69	43	49	37	36	47
Total mortality, %	71	69	49	84a	67ab	62b	72
L'Acadie, 1993							
Number of hosts[a]	5	0	8	122	70	105	310
C. glomerata, %	20	-	0	12	16	11	12
C. rubecula, %	0	-	0	16	26	19	18
Total parasitism, %	20	-	0	27	41	30	30
Diseases, %	40	-	38	39	26	36	35
Total mortality, %	60	-	38	66	67	66	65
L'Acadie, 1994							
Number of hosts[a]	11	4	21	397	337	219	989
C. glomerata, %	0	0	0	5	5	5	5
C. rubecula, %	9	50	10	19c	26b	63a	31
Total parasitism, %	9	50	10	23c	31b	68a	36
Diseases, %	18	0	5	30a	13b	11b	19
Total mortality, %	27	50	15	53b	44b	79a	55

Percentages within a row and for the same cropping period, followed by the same letter are not significantly different: *G* test followed by STP procedures, $P > 0.05$.

[a] Total number of third instars collected.

Table 4.5: Major mortality factors (%) of *A. rapae* pupae on broccoli, cabbage, and Brussels sprouts during 1993-1994

	Early crops			Late crops			
	Broc.	Cab.	B.spr.	Broc.	Cab.	B.spr.	Total
Ste-Clotilde, 1993							
Number of hosts[a]	2	5	7	14	15	13	56
P. vulgaris, %	0	20	0	0	13	0	5
P. puparum, %	0	0	0	14	7	0	5
Total parasitism, %	0	20	0	14	20	0	11
Diseases, %	0	40	29	14b	27ab	62a	32
Total mortality, %	0	60	29	29	47	62	43
L'Acadie, 1993							
Number of hosts[a]	3	8	2	107	122	107	349
P. vulgaris, %	0	13	0	24	22	16	20
P. puparum, %	0	0	0	4b	9b	31a	14
Total parasitism, %	0	13	0	28b	31ab	47a	34
Diseases, %	0	25	0	35ab	43a	22b	33
Total mortality, %	0	38	0	63	75	68	67
L'Acadie, 1994							
Number of hosts[a]	17	10	38	98	245	47	455
P. vulgaris, %	0	10	5	7ab	2b	21a	6
P. puparum, %	0	0	0	0	22	0	12
Total parasitism, %	0	10	5	7b	25a	21ab	18
Diseases, %	12	30	21	61a	54a	4b	46
Total mortality, %	12	40	26	68a	78a	26ab	63

Percentages within a row and for the same cropping period, followed by the same letter are not significantly different: *G* test followed by STP procedures, $P > 0.05$.

[a] Total number of pupae collected.

Table 4.6: Survival of *Plutella xylostella, Artogeia rapae*, and their parasitoids after five months at 4°C (at the pupal stage).

Species	Total	Alive	Dead
1993			
P. xylostella	7	0	7
M. plutellae	358	275	83 [a]
D. insulare	3	0	3
Cotesia sp	6	6	0
S. bilineatus	14	14	0
A. rapae	136	104	32
C. glomerata	5	0	5
C. rubecula	270	238	30 (2) [b]
P. vulgaris	2	0	2
1994			
P. xylostella	4	0	4
M. plutellae	67	27	40 [a]
D. insulare	20	0	20
A. rapae	304	237	67
C. rubecula	439	301	135 (3) [b]
P. vulgaris	28	10	18
P. puparum	2	2	0

[a] Dead pupae of *M. plutellae* have not been distinguished from *S. bilineatus* pupae.
[b] Number of pupae parasitized by *B. galactopus*.

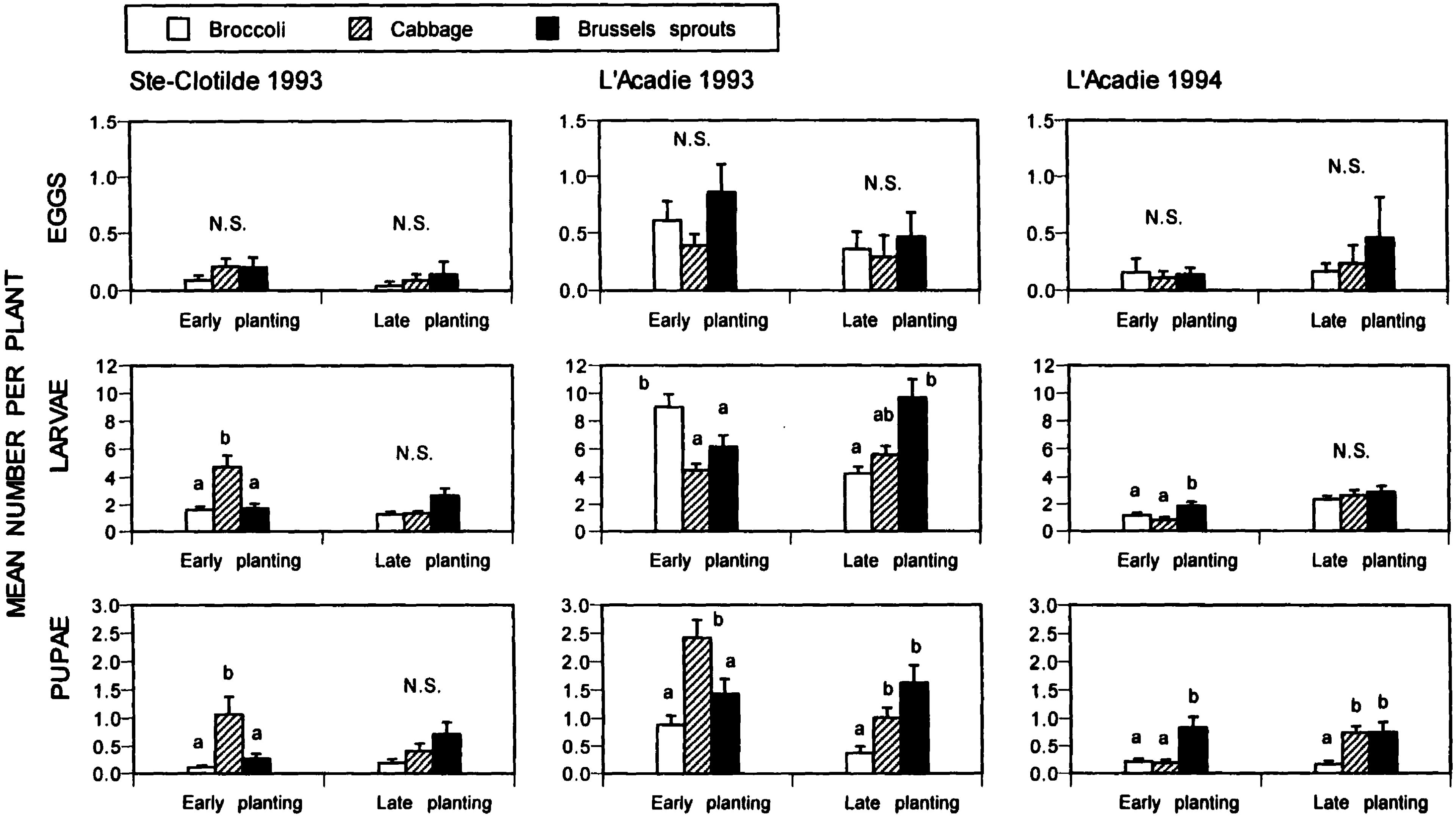


Figure 4.1: Mean numbers of eggs, larvae and pupae of *Plutella xylostella* on three cruciferous crops during 1993-94 in southwestern Quebec. Bars with the same letter are not significantly different at $P > 0.05$ (Tukey HSD on log-transformed data). Error bars are standard errors.

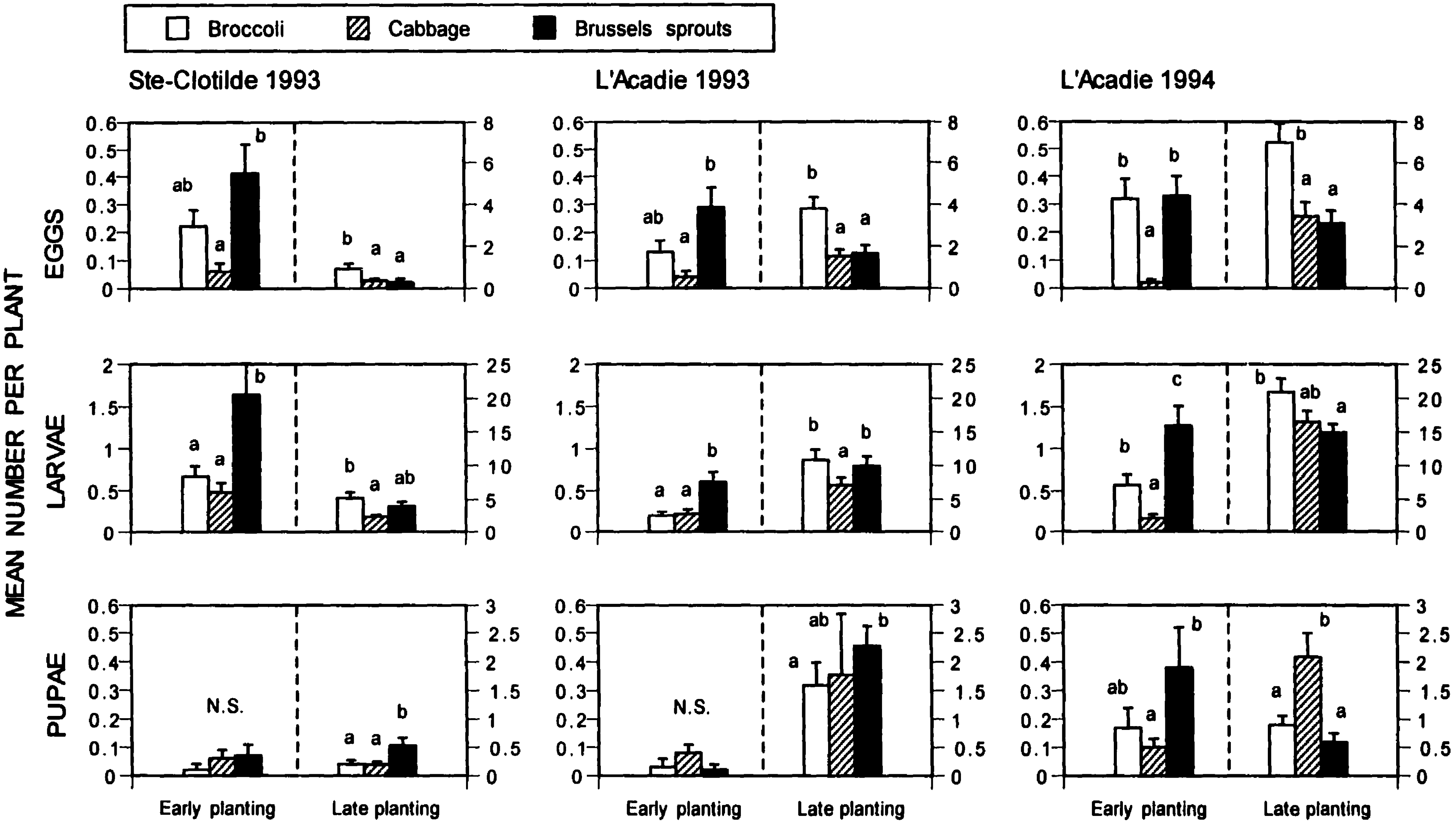
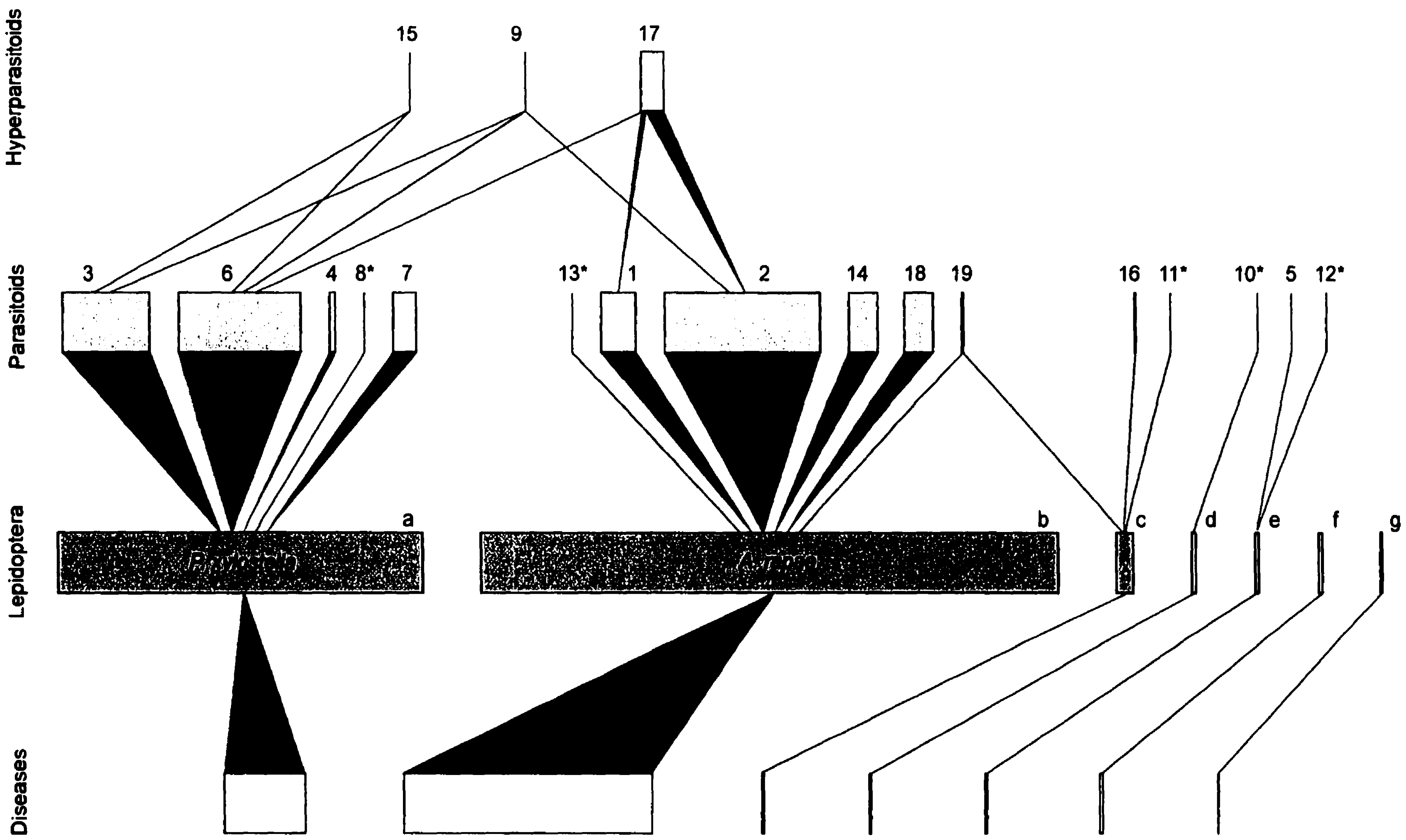


Figure 4.2: Mean numbers of eggs, larvae and pupae of *Artogeia rapae* on three cruciferous crops during 1993-94 in southwestern Quebec. Bars with the same letter are not significantly different at $P > 0.05$ (Tukey HSD on log-transformed data). Error bars are standard errors.

Fig. 4.3: Quantitative web for the *Brassica* crops parasitoid community. Species are represented by rectangles and their width is proportional to their abundances. Letters refer to Lepidoptera species: (a) *P. xylostella* (b) *A. rapae* (c) *T. ni* (d) *D. trifolii* (e) *X. c-nigrum* (f) *M. picta* (g) *E. acrea*. Numbers refer to parasitoid and hyperparasitoid species (listed in Table 1), and species followed by an asterisk were found only at one location during the study. Diseases are shown at the bottom of the figure.


Hyperparasitoids
15
9
17
Parasitoids
3
6
4
8*
7
13*
1
2
14
18
19
16
11*
10*
5
12*
Lepidoptera
a
b
c
d
e
f
g
Diseases

Connecting text

We showed in the preceding chapter that the ICW was the most important lepidopterous pest in southwestern Quebec, followed by the DBM and the CL. The *Brassica* varieties appeared to influence the level of infestation by the ICW, as broccoli was preferred over cabbage and Brussels sprouts. In addition, several parasitoid species were found on each plant variety, but were insufficient to protect the crops. Thus, cruciferous crops cannot be economically produced without measures to control the lepidopterous pests.

No indigenous egg parasitoids were regularly found, which would have served in the establishment of more laboratory colonies to work with. On the other hand, this leaves the egg stage of the pests as an opportunity for the intervention to control the pests at an early stage with egg parasitoids.

Concurrently to these field studies, laboratory experiments were carried out on several Trichogrammatidae species obtained from various parts of the world. The first steps in the selection of the most promising species include host preference studies. Ideally, the perfect species would not discriminate between the three lepidopterous pests, and would accept eggs of any development stage. A methodology was developed and laboratory experiments were performed on these two aspects of host selection, the host age selection being the subject of the following chapter.

This chapter will be submitted for publication in the journal **Entomologia Experimentalis et Applicata.**

V. PROGENY AND SEX ALLOCATION BY TRICHOGRAMMATIDAE SPP IN RESPONSE TO HOST AGE AND SPECIES

Abstract

The impact of two host quality factors, host age and species, on the parasitism rates, host suitability, progeny and sex allocation of several Trichogrammatidae (Hymenoptera) species/strains was examined in laboratory choice tests. Individual female parasitoids were provided with young, medium-aged and old eggs of one of three Lepidopterous host species: *Trichoplusia ni* (Hübner) (Noctuideae), *Artogeia rapae* (L.) (Pieridae), and *Plutella xylostella* (L.) (Plutellidae). Trichogrammatidae species behaved as gregarious parasitoids with the first two host species, and as solitary parasitoids with the smaller *P. xylostella*. Most Trichogrammatidae species/strains significantly preferred to parasitize young *T. ni* eggs, whereas they showed no discrimination between *A. rapae* egg ages, and often preferred young or medium-aged *P. xylostella* eggs. However, host suitability was generally not related to parasitism rates, as no differences were found between host ages for this factor, whereas substantially low suitability was regularly observed in *A. rapae* eggs. In contrast, a decreasing number of offspring per host was frequently observed in older eggs, although not always significantly different, for both *T. ni* and *A. rapae*. Offspring sex ratio did not appear to be manipulated at all in *T. ni* and *A. rapae* eggs, and rarely in *P. xylostella* eggs, with no particular trend. These results are in agreement with optimal foraging theoretical predictions, in regard to host age, only for *T. ni*, for which the females Trichogrammatidae parasitized fewer old eggs and reduced the number of offspring in them.

Key words: *Artogeia rapae*, *Plutella xylostella*, *Trichoplusia ni*, *Trichogramma*, *Trichogrammatoidea*, egg parasitoids, natural enemies, host age, host quality, sex ratio, progeny allocation, optimal foraging

Introduction

When a female parasitoid discovers a host patch, it must select which hosts to parasitize. The optimal foraging theory (OFT) predicts that foragers encountering various hosts will show a preference for the most profitable type of host, i.e. the one providing maximal survival and fitness to the progeny (Pyke et al. 1977). OFT assumes that the fitness associated with an animal's foraging behavior has been maximized by natural selection and that foragers can make decisions so as to maximize their gain of fitness, which translates into the rate of oviposition for parasitoid wasps (Charnov & Skinner 1985).

A female parasitoid must 'decide' how many eggs to lay in available hosts and, in the case of hymenopterous parasitoids, what sex to produce (Waage & Godfray 1985). The reproduction strategy of a female includes both progeny and sex allocation (Nadel & Luck 1992), and optimality models have been developed based on the natural selection approach to oviposition decisions (Charnov & Skinner 1985; Waage & Godfray 1985; Waage 1986; Godfray et al. 1991).

The number and sex of the eggs allocated to a host during oviposition vary with the female's assessment of host size, age, nutritional suitability and previous parasitization (Schmidt 1994). In gregarious parasitoids, adult size decreases as the number of developing progeny increases in a given host (Klomp & Teerink 1962; Waage & Ng 1984; Bai et al. 1992; Kazmer & Luck 1995) and, since the size of a parasitoid directly affect its fitness (Waage & Ng 1984), optimality models predict that females will allocate different numbers of eggs when encountering hosts varying in quality, in order to optimize the size and fitness of their progeny (Charnov & Skinner 1984, 1985; Waage & Godfray 1985; Godfray et al. 1991). In non-growing hosts, if clutch size increases with increasing host quality, the resources available to a developing wasp will not be directly related to host quality, but rather limited by the presence of the other developing wasps. For this reason, sex ratio manipulation in response to host quality is not expected in gregarious idiobiont parasitoids (King 1987, 1993).

In solitary parasitoids, females cannot adjust the resources available to their progeny by varying the number of larvae developing per host, so that adult size is correlated with host size (King 1987, 1989). This relation also applies to other host quality factors such as host age and species (Vinson & Iwantsch 1980; Waage & Ng 1984; Ruberson & Kring 1993). If we assume that being small is less disadvantageous to the reproductive success of males than of females (Charnov et al. 1981), the Charnov's host quality model predicts that mothers should produce a greater proportion of sons under conditions that will result in smaller offspring. In addition, the response of the parasitic wasp to a particular host quality will depend upon the other hosts available (Charnov 1979; Charnov et al. 1981; Hails 1989; King 1992).

Theoretical models have focused primarily on females manipulating the size and sex ratio of their progeny in response to host size and/or female density (King 1987). However, hosts such as eggs and pupae are expected to provide fewer resources with increasing age, because nutrients are metabolized or converted into substances which cannot be assimilated by developing parasitoids (Ruberson et al. 1987; King 1990). In idiobiont parasitoids, older hosts are often less accepted and progeny survival is reduced in such hosts. As a consequence, females will tend to allocate fewer eggs to older hosts compared with young hosts (Lewis & Redlinger 1969; Marston & Ertle 1969; Taylor & Stern 1971; Parker & Pinnell 1974; Vinson 1976; Vinson & Iwantsch 1980; Juliano 1982; Pak & Oatman 1982).

The genus *Trichogramma* and *Trichogrammatoidea* (Hymenoptera: Trichogrammatidae) are egg parasitoids widely used in biological control programs (Hassan 1993), whose characteristics make them suitable candidates to test optimality models predictions. Egg parasitoids use hosts which size do not vary with time and females are known to adjust sex ratio to the size of the host available (King 1989; Waage 1982). Schmidt & Smith (1987) demonstrated that ovipositing *T. minutum* (Riley) females judge host size in relative terms and Suzuki et al. (1984) found that competition between larvae of *T. chilonis* (Ishii) does not regulate clutch size, a factor that could interfere with sex allocation predictions. Genetic variability in progeny and sex allocation has been found between individuals of *Trichogramma* species, which is a prerequisite for natural selection to operate (Wajnberg et al. 1989; Wajnberg 1990, 1994).

While a host egg does not vary in size over time, its quality as host will change as the embryo develops. In *Trichogramma*, acceptance of host eggs will change (Pak 1986) and nine types of relationship can be modeled (Fig. 1). Usually, host acceptance, successful development of parasitoid larvae, and fecundity of emerging females, which could be taken as an indication of fitness, decrease with host age (type I, II & III in Fig. 1). Young hosts are accepted more readily than older hosts, and sclerotization of the head capsule of the host embryo often marks the end of host acceptability (Schmidt 1994). Large differences in host age effect between *Trichogramma* species are reported in the literature (Pak 1986), but some of these may be related to variations in experimental protocols (Hintz & Andow 1990). In the majority of these studies, females are tested in a no-choice situation, despite that choice tests are the most straightforward and appropriate preference tests (King 1993).

In this study, the effect of host age on parasitism rates, host suitability, and progeny and sex allocation, was evaluated in 42 species and strains of *Trichogramma* and *Trichogrammatoidea*. The impact of host size on the response to host age was studied by using three different lepidopterous host species: the cabbage looper (CL), *Trichoplusia ni* (Hübner) (Noctuidae); the imported cabbageworm (ICW), *Artogeia* (*=Pieris*) *rapae* (L.) (Pieridae); and the diamondback moth (DBM), *Plutella xylostella* (L.) (Plutellidae). These three species are pests of cruciferous crops in North America (Harcourt 1963). The CL and ICW eggs are relatively similar in size, the CL egg being spherical and the ICW egg bullet-shaped, while the ellipsoid DBM egg is much smaller. The volume of the eggs were estimated as 0.62 mm^3, 0.61 mm^3, and 0.13 mm^3 for the CL, ICW and DBM, respectively (Harcourt 1957; Hohmann et al. 1988; Pak et al. 1986).

Trichogramma and *Trichogrammatoidea* species are facultatively gregarious, and several wasps usually develop into CL and ICW eggs. DBM eggs are the smallest of the three species used, and only one *Trichogramma* usually develops per egg. In the case of DBM, host quality models predict that the female should oviposit more females into high quality hosts, and males in low quality hosts. However, no modification in sex allocation is expected with the CL and ICW eggs. We rather hypothetize that the ovipositing female will adjust the number of eggs allocated in hosts of varying age, laying more eggs in young hosts compared with old hosts. Finally, an attempt was made to extend the use of standardized relationship types introduced by Pak (1986) to classify parasitism rates and other factors related to host age (Fig. 1).

Materials and methods

Host species

Laboratory cultures of CL, ICW, and DBM were maintained on artificial diets (Shorey & Hale 1965; Webb & Shelton 1988; Shelton et al. 1991) at 23 ± 1°C, 65 ± 5% r.h. and L16:D8. In these conditions, egg development of CL, ICW and DBM lasted about 96, 96, and 84 hours, respectively. Different oviposition media were used to collect eggs from the three species: sheets of waxed paper for the CL, strips of plastic film for the ICW, and the plastic side of polythene coated absorbent paper (previously dipped in a filtered cabbage juice) for the DBM. Eggs were collected daily, put in plastic bags and kept at the previously mentioned conditions until used for experiments. The developing eggs were classified into three categories: young, medium-aged and old eggs. The categories used were 2, 44 and 74 ± 2 hours old eggs for CL and ICW, and 2, 28 and 68 ± 2 hours old eggs for DBM.

Parasitoid species/strains

We used a collection of 42 species and strains of *Trichogramma* and *Trichogrammatoidea*, most of them arrhenotokous, and originating from various geographic locations (Table 1). We used the species identifications provided by the cooperators who supplied us with the initial Trichogrammatidae stock.

Trichogrammatidae species/strains were reared on a factitious host, the Mediterranean flour moth, *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) whose eggs had a volume of 0.28 mm^3 (Bai et al. 1992), and in which usually one parasitoid could develop. Cold-killed *E. kuehniella* eggs were glued on paper strips, and placed into glass shell vials whose open end was sealed by a paper plug. Temperature was maintained at 23 ± 1°C, with 65 ± 5% r.h., and L16:D8 photoperiod. Under these conditions, Trichogrammatidae development lasted 11 to 14 days, depending on the species/strain, and most of the adult emergence occurred in the first three hours of the photophase. Trichogrammatidae females used were 3 ± 1 hours old, mated and had no previous oviposition experience with the three host species.

Experimental design

An inverted plastic petri dish (35.0 mm diameter) was used as the experimental arena, with a 42.5 mm filter paper disk fitted into the bottom of the device. Eggs of the three age classes were placed on the filter paper along a 6 x 6 Latin square design for the CL and the ICW, for a total of 36 eggs. Because only one egg is laid into DBM eggs, more hosts can be parasitized during the same period of time. For this reason, a series of three eggs was added along the four margins, giving a total of 48 DBM eggs. The distance between individual eggs was 4.0 mm, allowing the placement of a plastic grid that isolates them (see below).

One female parasitoid was introduced in the center of the arena using a wet paint brush, and the petri dish was closed and sealed with parafilm. The wasp was removed after a four hour exposure period at 25 ± 1°C. A 1.2 mm thick flexible plastic grid, with 2.0 mm diameter holes corresponding to the position of the eggs, was then placed on the filter paper. To keep the eggs from moving, the petri dish section previously used as the cover was inverted over the grid and held in place by two rubber bands. This device isolated the eggs into individual cells without direct manipulation. The petri dishes were placed on a tray and enclosed into a transparent plastic bag containing a wet sheet of blotting paper to keep a high humidity level. Incubation at 25 ± 1°C and 16D:8L lasted until adult parasitoid emergence, at which time the number and sex of emerging adults were recorded, along with the number of dead host eggs.

Each day, a petri dish was used as control treatment, prepared as previously mentioned, but without parasitoid. During an experiment, if the mortality observed in the control treatment reached 25%, the associated replicates were discarded from the analysis. For a given lepidopterous species, any Trichogrammatidae species/strain that failed to parasitize at least five host eggs during five consecutive replicates was excluded from the analysis (missing numbers of replicates in Table 1). Finally, when only males were produced in a replicate, these data were not used as it indicated that the ovipositing female had not mated.

Data analysis

The effective host mortality, which is the number of host eggs in which embryonic development was interrupted by the parasitoid, was calculated using the following formula: (number of hosts from which parasitoids emerged) + ((number of dead host eggs exposed to the parasitoid, but without adult parasitoid progeny) – (number of host eggs dead in the control treatment)). If the number of host eggs dead in the control treatment was superior to the number of dead host eggs exposed to the parasitoid, the negative number resulting in the formula was replaced by 0. This correction was used to avoid underestimation of the number of hosts killed from which parasitoids emerged.

Number of progeny per host and sex ratios were used for analysis only when at least one adult wasp emerged from every host age class. Host suitability is defined as the estimated proportion of host eggs killed by the female parasitoid and from which at least one adult parasitoid emerged. The sex ratios are reported as the proportion of females. For all analysis, we compared the three age classes using a Friedman two-way analysis of variance by ranks (Daniel 1990). Significant differences in the response of the Trichogrammatidae species/strains to host age were used to classify the results according to the nine types of relationship (Fig. 1).

Results

Hosts killed by the parasitoid

The CL eggs were accepted as host by all 42 species/strains of Trichogrammatidae (Fig. 2). Fourteen strains showed no significant preference for a particular host age (type I, Fig. 2a), whereas younger hosts were preferred by most (28) species/strains (Fig. 2b, c). The youngest hosts were preferred over medium and old hosts by 15 species/strains (type III and V), and except in one case (strain #25), the number of young eggs parasitized was significantly higher than for medium and old eggs, which had similar level of parasitism. Some species/strains were extremely selective in parasitizing up to three times more young eggs than medium-aged and old eggs combined (#30, #35, Fig. 2c). Finally, the lowest host mortality occurred on medium-aged hosts in 13 species/strains (type IV, Fig. 2b), and this host-age relationship was found only in CL eggs, with the exception of one strain in ICW eggs (Fig. 3b).

The ICW eggs were less accepted as hosts and only 30 species/strains out of the 42 showed constant parasitism (Fig. 3). A large majority of these showed no preference for any age class (24/30, type I, Fig. 3a). Five strains showed a preference for young eggs over medium-aged or old eggs (types III, IV and V relationships), while one strain preferred medium-aged eggs (type VI, Fig. 3b). The species/strains that preferred the younger ICW eggs (#7, #11, #23, #28, #37) had also shown such a preference with CL eggs (Fig. 2 and 3).

Only 21 of the 42 available species/strains parasitized enough DBM eggs for analysis (Fig. 4). Twelve species/strains showed no significant differences in the number of hosts killed per age class (type I, Fig. 4a). In contrast, young and medium-aged eggs were preferred over old eggs for four strains (#10, #35, #38, #39) (type II), while the medium-aged class was the preferred host age (type VI) for five other strains (#2, #6, #8, #20, #25) (Fig. 4b). Apart from three strains (#6, #8, and #20), those preferring young or medium-aged DBM eggs also showed a preference for younger hosts when CL eggs were offered (Fig. 2), but showed no preference in the case of the ICW (Fig. 3).

Host suitability

Analysis of suitability was performed only when one or more eggs were parasitized in each age class within a given replicate, a condition that reduced the number of species/strains retained for analysis when the parasitism levels were low.

In CL eggs, data were analyzed for 32 species/strains in which suitability ranged from 27% to 100% (Table 2). For most of the Trichogrammatidae species/strains, eggs of all ages were equally suitable for parasitoid development (type I, Table 2). However, a significant decrease occurred in older eggs for five species/strains (#2, #13, #22, #29, #42) (types II and V, Table 2), while an increase of suitability occurred in older eggs for strains #6 and #20 (types VI and VIII, Table 2). Lower host suitability in older CL eggs was found in species/strains for which the number of hosts parasitized also decreased with host age (#2, #22, #29, #42) (types II and V in Table 2; types IV and V in Fig. 2). However, host suitability was generally not associated with differences in the number of hosts killed, since for 21 species/strains discriminating between different CL egg ages, 17 did not show significant difference in suitability between the three age classes (types III, IV and V in Fig. 2; type I in Table 2).

Suitability of ICW eggs was analyzed for 19 species/strains, and ranged from 0% to 88% (Table 3). Although ICW eggs were stung by the remaining 11 species/strains (Fig. 3), no adult offspring emerged, while three strains in Table 3 barely completed development (#4, #9, #33), indicating that ICW eggs are unsuitable hosts for several Trichogrammatidae species/strains. ICW eggs and a close relative to the ICW, *Pieris brassicae* (L.), were also found to be unsuitable for Trichogrammatidae development (Parker & Pinnell 1974; Pak & van Lenteren 1984; Pak et al. 1990). The relationship between ICW egg ages and host suitability was usually not significant (type I, Table 3). However, when we found differences (#2, #23, #27), the lowest suitability was found in young ICW eggs (types VI and IX, Table 3). Thus, when restrained with ICW eggs, several Trichogrammatidae species/strains killed a substantial number of hosts by either stinging or ovipositing, despite unsuitability for larval development. No particular relationship between parasitism and suitability of ICW eggs was found, and in general both parasitism and suitability were not different between host ages (type I, Fig. 3; Table 3). It should be noted that a high suitability was found in two strains initially recovered from ICW eggs (#2 and #3, Tables 1 and 3).

In DBM eggs, data were analyzed for 19 species/strains in which suitability ranged from 30% to 96% (Table 4). The medium-aged DBM eggs were more suitable for development than one or both of the other age classes, for eight species/strains (type II, VI and IX, Table 4), which might explain the high levels of parasitism usually found for this age class (types II and VI, Fig. 4). The other 11 species/strains showed no significant difference between DBM eggs of all ages (type I, Table 4).

Progeny allocation

Progeny allocation in CL eggs was analyzed for 23 species/strains, where the average number of adults emerging per egg varied between 1.14 and 2.98 (Table 5).

Fourteen species/strains showed a significant decrease in number of progeny according to CL egg ages (types II, III and V, Table 5), and only one (#8) increased the number of its progeny in medium-aged eggs (type VI, Table 5). The other eight species/strains had no significant differences in progeny allocation (type I, Table 5), although for all 23 strains there was a tendency for the lowest progenies to be associated with the oldest age class (Table 5).

Twelve of these 23 species/strains parasitized preferentially young CL eggs (types IV and V, Fig. 2), and of those, a majority (9/12) also allocated more offspring into the youngest hosts encountered, and fewer offspring into older hosts (types II, III and V, Table 5). Strains #13 and #20 were the only ones for which a significant decrease in progeny allocation with host age (type III, Table 5) was associated with different host suitability (types II and VIII, Table 2). However, the number of hosts killed was not significantly different between CL egg ages for these two species/strains (type I, Fig. 2).

Only five strains produced enough adult offspring in ICW eggs for analysis, and the average number of adults emerging per egg varied between 1.75 and 3.14 (Table 6). This range in progeny allocation is similar to the one observed in CL eggs (Table 5), which are similar in size but different in shape when compared with ICW eggs. Although there was a tendency for more progenies being allocated in young ICW eggs, the difference was significant in only one strain (#23, type III, Table 6). This strain was the only one that also showed different parasitism rates and host suitability according to ICW eggs age (type VI, Table 3; type V, Fig. 3). However, the suitability was the lowest in the youngest eggs, the age class preferred for both number of hosts killed and progeny allocation.

In DBM eggs, number of progenies was restricted to one adult parasitoid per egg, so only sex allocation will be discussed for this species (see below).

Sex allocation

Sex allocation in CL and ICW was analyzed for the same strains as for progeny allocation. All sex ratios were female-biased, varying between 0.60 ± 0.07 (strain #14) to 0.97 ± 0.02 (strain #41) in CL eggs, and between 0.69 ± 0.10 (#24) to 0.88 ± 0.06 (#26) in ICW eggs. We found no indication that females manipulated sex allocation according to host age in either CL or ICW eggs, as none of the species/strains showed significant differences between host ages (type I relationship).

Sex allocation in DBM eggs was analyzed for the same strains as for suitability. Most, but not all, sex ratios were female-biased, with averages varying from 0.39 ± 0.10 (#29) to 1.00 (#25). Contrarily to CL and ICW eggs, sex ratios reaching values below 0.60 were found in DBM eggs for eight of the 19 species/strains analyzed (#5, #14, #15, #23, #29, #34, #36, #38). Only three species/strains showed significant differences in sex allocation according to DBM eggs ages. These strains had three different types of relationship: IV, VI, and VIII types (proportions of females in young, medium-aged and old eggs: 0.71 ± 0.06, 0.64 ± 0.04, 0.76 ± 0.04 for #6, N=17, χ^2=6.18 , $p<0.05$; 0.50 ± 0.08, 0.87 ± 0.05, 0.74 ± 0.11 for #23, N=9, χ^2=10.97 , $p<0.004$; and 0.53 ± 0.09, 0.69 ± 0.05, 0.84 ± 0.05 for #34, N=15, χ^2=11.31 , $p<0.004$). Strain #6 was the only one showing both differential parasitism (type VI, Fig. 4), host suitability (type IX, Table 4) and sex ratio manipulation (type IV) in response to DBM eggs age, whereas strain #34 had differential suitability (type VI, Table 4) and sex ratio (type VIII). Although the suitability of young DBM eggs was the lowest for these two strains, only strain #34 laid more males in young eggs.

Discussion

Hosts killed by the parasitoid and host suitability

For the first time, host-age selection by Trichogrammatidae was studied, using a single methodology, in a choice situation and on three host species. We used 42 species/strains of Trichogrammatidae of geographically diverse origins, and therefore these results should be representative of the response to host age in this family.

The reported facts that host-age preference is a common phenomenon in Trichogrammatidae, and that variations occur between Trichogrammatidae species and host species (Pak 1986) is further supported by our study. Preference of Trichogrammatidae for young eggs (type II, III, and V relationships, Fig. 1) appeared widespread among Trichogrammatidae species/strains, as observed by Pak (1986), but there was not a dominant relationship type representative for all host species. Several reasons may explain higher parasitism rates in the preferred host age. Less preferred hosts can be rejected upon contact by the female or after it has inserted its ovipositor (Marston & Ertle 1969). Host handling time may also vary between host ages, resulting in fewer parasitized hosts when handling time is longer. In this view, van Huis et al. (1991) showed that the time needed for penetrating the egg chorion increased with host age in *Uscana lariophaga* Stephan (Trichogrammatidae).

The particular low acceptance level of medium-aged eggs as compared with young and old eggs found with the CL (type IV) is also reported in other studies on Trichogrammatidae (Marston & Ertle 1969; Parker & Pinnell 1974), and for a polyembryonic Encyrtidae, *Copidosoma truncatellum* (Dalman) using the same host species (Stoner & Weeks 1976). Marston & Ertle (1969) noted that inhibition of acceptance of CL eggs coincided with blastokinesis or rotation of the host embryo, and showed that the decreased parasitism for middle-aged CL eggs was due to a rejection of the host egg after insertion of the ovipositor, and not because of a higher mortality of the *T. minutum* larvae, which is consistent with our observations. However, other studies showed a type IV relationship in Trichogrammatidae for both oviposition and host suitability (Pak 1986), which tend to support the optimal progeny allocation theory. More detailed investigations are needed to clarify the link between CL eggs preference and suitability.

According to host species, our results suggest that preferences of certain host ages are expressed more often in hosts species that are highly suitable for parasitoid development. Most Trichogrammatidae species/strains showed different numbers of hosts killed between young and old eggs in highly suitable CL eggs, as opposed to only a few species/strains in eggs of ICW. It is consistent with OFT that low response levels to host age are observed in a barely suitable host, such as the ICW egg (Vet et al. 1990). Female parasitoids are not expected to discriminate between different host ages when the relative differences in quality between different ages are offset by the low quality of the species as a host.

Progeny and sex allocation

Only secondary sex ratios were measured in this study and this could have introduced a bias as the decision of the female is best represented by the primary sex ratio. However, differential mortality of male and female larvae is a significant factor for Trichogrammatidae only when superparasitism is important (Schmidt 1994), which was not the case in this study as hosts were provided in excess to the oviposition capacity of the females.

Our results support the progeny and sex allocation theory in the case of gregarious egg parasitoids (Godfray et al. 1991; King 1993). The number of progenies per host decreased with host age, and type II and III relationships were the most common, which suggest that host quality decreased with age and that the ovipositing females were able to detect it. As expected from theoretical predictions (King 1993), arrhenotokous Trichogrammatidae females did not modify the sex-ratio of their progeny in relation to host age when the host could sustain more than one offspring (CL and ICW).

Concerning the female-biased sex ratio that we constantly observed, the LMC models predict that, when a female wasp is alone on a host patch, a female biased sex ratio is produced because the ovipositing female allocates just enough sons to inseminates all her daughters (Hamilton 1967; van Welzen & Waage 1987; Nadel & Luck 1985, 1992).

When a female parasitoid of a solitary or facultatively gregarious species allocates resources between different hosts in which only one parasitoid can develop, it is expected that more males are allocated in the least preferred hosts (Charnov 1979; Charnov et al. 1981). Our results did not support this prediction as similar proportions of males were allocated in the different DBM eggs ages. However, other studies on Trichogrammatidae showed that males are allocated early in an oviposition sequence, a factor that can be independent of host quality (Waage & Ng 1984). Females of *T. evanescens* (Westwood) (Waage 1986), *T. chilonis* (Suzuki et al. 1984) laid male eggs in the second or third host egg parasitized irrespective of clutch size. This behavior, independent of host age, is probably widespread among Trichogrammatidae (G. Boivin, unpublished data) and may explain that no differences of sex ratios were observed between host ages. Finally, the DBM eggs could be considered as low quality hosts for Trichogrammatidae species, as their size limits the development of female progeny as shown by the low survival rates and the high sex ratios observed. A larger host, such as *E. kuehniella*, would probably be more appropriate to study sex allocation in Trichogrammatidae.

In conclusion, the overall preference for young host eggs, combined with larger clutch size in such young hosts, underlines the importance of considering host age when undertaking selection tests for biological control programs or host preference tests. Host age will also influence mass production of parasitoids, especially in large hosts such as CL eggs, as the production can be severely reduced in older eggs. Furthermore, host age should be considered when other aspects of OFT are studied for theoretical considerations.

We showed that, in absence of superparasitism, females Trichogrammatidae detect host age and, when the host species is highly suitable for larval development, respond generally by parasitizing preferentially young hosts, and by reducing the size of their progeny with increasing host age. The progeny sex ratio is usually not adjusted by the mother wasp in response to host age. Sex ratio adjustment in Trichogrammatidae is more likely related to the sequence of egg laying than to a response to host quality. Finally, if the time needed by a female wasp to pierce the egg chorion increases with host age, it is possible that the resulting longer handling time induces a reduction in the number of eggs laid. A longer handling time may also explain the lower parasitism rates observed in older eggs, but more detailed behavioral observations are necessary to confirm this statement.

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Table 5.1: List of *Trichogramma* and *Trichogrammatoidea* species/strains used in host age preference tests, and associated initial number of replicates. Species #1, #11, #12 and #42 are thelytokous, the others are arrhenotokous

				Number of replicates		
Strain	Species	Host	Origin	CL	ICW	DBM
1	*T. sp.*	*Pieris brassicae*	Iran	10	12	-
2	*T. sp.*	*Artogeia rapae*	France	15	10	12
3	*T. sp.*	*Artogeia rapae*	France	11	10	-
4	*T. pretiosum* Riley	*Ephestia kuehniella*	Québec	11	10	-
5	*T'dea. bactrae* Nagaraja	-	Thailand	11	-	11
6	*T'dea. bactrae* Nagaraja	*Plutella xylostella*	Thailand	10	10	17
7	*T. brasiliensis* Ashmead	*Mamestra brassicae*	Germany	13	10	-
8	*T. brassicae* Bezdenko	*Ostrinia nubilalis*	Italy	10	-	16
9	*T. pretiosum* Riley	*Ephestia kuehniella*	Québec	13	10	-
10	*T. buesi* Voegelé	*Mamestra brassicae*	France	13	10	11
11	*T. cacoeciae* Marchal	*Lobesia botrana*	Italy	12	10	-
12	*T. cacoeciae* Marchal	*Sitotroga cerealella*	Germany	11	-	-
13	*T. chilonis* Ishii	*Autographa nigrisigna*	Japan	10	-	-
14	*T. chilotrae*	*Chilo suppressalis*	Thailand	10	-	10
15	*T. chilonis* Ishii	-	India	15	11	10
16	*T. confusum* Viggiani	*Antherea pemyi*	France	11	-	-
17	*T. cordubensis* Vargas & Cabello	-	Azores	10	-	-
18	*T. cordubensis* Vargas & Cabello	-	Iran	10	10	-
19	*T. deion* Pinto & Oatman	Hesperidae	USA	10	10	-
20	*T. dendrolimi* Matsumura	-	Romania	11	10	11
21	*T. dendrolimi* Matsumura	*Ostrinia nubilalis*	Bulgaria	12	10	-
22	*T. embryophagum* Hartig	-	-	12	10	-
23	*T. evanescens* Westwood	-	Egypt	13	10	10
24	*T. evanescens* Westwood	*Mamestra brassicae*	Italy	13	11	-
25	*T. leptoparameron*	-	ex USSR	10	-	9
26	*T. sp.*	-	Madeira	8	8	-
27	*T. brassicae* Bezdenko	*Ostrinia nubilalis*	Moldavia	10	9	-
28	*T. brassicae* Bezdenko	*Mamestra brassicae*	ex USSR	12	8	7
29	*T. minutum* Riley	*Choristoneura fumiferana*	Ontario	12	-	10
30	*T. minutum* Riley	*Rhopobota naevana*	British Columbia	10	-	-
31	*T. minutum* Riley	Sphingidae	USA	16	-	-
32	*T. minutum* Riley	*Danaus plexippus*	USA	10	11	8
33	*T. pretiosum* Riley	*Ephestia kuehniella*	Québec	14	8	-
34	*T. ostriniae* Pang & Chen	-	-	13	10	16
35	*T. pintoi* Pintureau & Voegelé	-	China	13	9	13
36	*T. pretiosum* Riley	*Heliothis zea*	USA	13	10	12
37	*T. pretiosum* Riley	*Agraulis vanillae*	USA	10	9	10
38	*T. pretiosum* Riley	*Diatrae saccharalis*	Bolivia	10	10	10
39	*T. principium* Sugonyaev & Sorokina	-	China	11	12	12
40	*T. semifumatum* Perkins	-	India	11	10	9
41	*T. pretiosum* Riley	*Ephestia kuehniella*	Québec	14	8	11
42	*T. sibericum* Sorokina	*Rhopobota naevana*	British Columbia	18	-	-

Table 5.2: Mean suitability of young (Y), medium aged (M), and old (O) cabbage looper eggs for Trichogrammatidae species/strains. Means followed by different letters are statistically different at $P < 0.05$ (Friedman two-way nonparametric analysis of variance by ranks)

Strain	N	Host age	% Suitability ± s.e.		Type	Strain	N	Host age	% Suitability ± s.e.		Type
1	6	Y	49.2 ± 12.4			21	9	Y	66.4 ± 6.1		
		M	36.1 ± 17.4	NS	I			M	88.3 ± 4.0	NS	I
		O	33.3 ± 21.1					O	68.0 ± 11.2		
2	10	Y	88.0 ± 6.6	a		22	10	Y	88.8 ± 5.0	a	
		M	31.7 ± 12.8	b	V			M	72.6 ± 10.3	a	II
		O	48.3 ± 15.0	ab				O	26.6 ± 7.6	b	
3	6	Y	88.9 ± 7.0			23	12	Y	92.4 ± 4.0		
		M	83.3 ± 16.7	NS	I			M	86.8 ± 5.9	NS	I
		O	100.0 ± 0.0					O	88.4 ± 5.0		
4	10	Y	83.7 ± 5.5			24	10	Y	77.3 ± 7.4		
		M	89.6 ± 5.6	NS	I			M	71.7 ± 13.2	NS	I
		O	72.3 ± 8.6					O	95.0 ± 5.0		
5	11	Y	58.9 ± 10.0			26	6	Y	100.0 ± 0.0		
		M	69.6 ± 12.3	NS	I			M	76.7 ± 15.0	NS	I
		O	55.6 ± 10.1					O	69.4 ± 13.9		
6	9	Y	53.0 ± 10.8	a		27	7	Y	81.9 ± 9.9		
		M	97.5 ± 2.5	b	VI			M	71.4 ± 18.4	NS	I
		O	80.2 ± 5.8	ab				O	48.8 ± 11.8		
7	11	Y	80.9 ± 6.4			28	10	Y	90.0 ± 3.8		
		M	65.2 ± 12.0	NS	I			M	70.8 ± 11.3	NS	I
		O	58.9 ± 11.9					O	76.7 ± 7.6		
8	9	Y	48.3 ± 11.7			29	11	Y	62.5 ± 9.2	a	
		M	81.3 ± 8.8	NS	I			M	30.4 ± 10.0	b	V
		O	90.3 ± 5.8					O	31.5 ± 9.1	ab	
9	12	Y	72.9 ± 7.8			31	13	Y	85.1 ± 5.6		
		M	74.6 ± 8.4	NS	I			M	59.1 ± 10.8	NS	I
		O	59.3 ± 10.3					O	60.2 ± 10.3		
11	6	Y	90.3 ± 6.2			33	10	Y	93.0 ± 5.2		
		M	72.2 ± 12.7	NS	I			M	65.7 ± 10.8	NS	I
		O	55.6 ± 20.5					O	64.2 ± 10.2		
13	8	Y	85.3 ± 7.6	a		34	12	Y	81.3 ± 4.8		
		M	84.4 ± 4.8	ab	II			M	91.2 ± 4.0	NS	I
		O	51.2 ± 10.9	b				O	74.7 ± 6.5		
14	10	Y	81.2 ± 6.0			36	11	Y	81.8 ± 6.0		
		M	88.0 ± 6.6	NS	I			M	81.5 ± 9.7	NS	I
		O	90.0 ± 6.7					O	74.0 ± 9.3		

15	13	Y	87.4 ± 5.1		
		M	73.1 ± 10.8	NS	I
		O	84.8 ± 6.6		
18	6	Y	64.3 ± 11.6		
		M	66.7 ± 15.4	NS	I
		O	84.7 ± 6.9		
19	7	Y	53.3 ± 13.6		
		M	75.0 ± 16.4	NS	I
		O	61.9 ± 14.9		
20	11	Y	61.6 ± 6.6	a	
		M	81.8 ± 5.6	ab	VIII
		O	90.0 ± 4.4	b	
37	8	Y	78.8 ± 9.0		
		M	80.0 ± 10.3	NS	I
		O	71.7 ± 7.5		
38	10	Y	73.1 ± 7.8		
		M	77.3 ± 5.9	NS	I
		O	86.3 ± 7.6		
41	12	Y	78.7 ± 6.6		
		M	73.3 ± 10.9	NS	I
		O	62.5 ± 12.3		
42	8	Y	92.4 ± 5.6	a	
		M	27.1 ± 14.1	b	V
		O	35.4 ± 12.8	ab	

Table 5.3: Mean suitability of young (Y), medium aged (M), and old (O) imported cabbageworm eggs for Trichogrammatidae species/strains. Means followed by different letters are statistically different at $P < 0.05$ (Friedman two-way nonparametric analysis of variance by ranks)

Strain	N	Host age	% Suitability ± s.e.		Type	Strain	N	Host age	% Suitability ± s.e.		Type
1	9	Y	11.1 ± 7.3	NS	I	26	7	Y	69.3 ± 15.9	NS	I
		M	56.7 ± 15.5					M	65.5 ± 9.2		
		O	22.6 ± 11.4					O	74.8 ± 12.0		
2	7	Y	10.0 ± 7.2	a	VI	27	9	Y	2.8 ± 2.8	a	IX
		M	88.1 ± 7.9	b				M	64.8 ± 9.7	b	
		O	43.7 ± 15.4	ab				O	48.1 ± 15.8	b	
3	10	Y	39.2 ± 11.8	NS	I	28	7	Y	70.9 ± 15.8	NS	I
		M	80.8 ± 11.3					M	59.8 ± 11.6		
		O	62.0 ± 13.7					O	45.7 ± 19.4		
4	8	Y	2.1 ± 2.1	NS	I	32	10	Y	20.3 ± 8.2	NS	I
		M	0.0 ± 0.0					M	62.1 ± 10.1		
		O	0.0 ± 0.0					O	60.0 ± 9.6		
7	8	Y	4.2 ± 4.2	NS	I	33	6	Y	4.2 ± 4.2	NS	I
		M	18.8 ± 13.2					M	3.3 ± 3.3		
		O	15.6 ± 10.5					O	0.0 ± 0.0		
9	9	Y	1.9 ± 1.9	NS	I	35	8	Y	4.2 ± 4.2	NS	I
		M	0.0 ± 0.0					M	14.4 ± 7.4		
		O	1.9 ± 1.9					O	18.8 ± 13.2		
10	8	Y	47.5 ± 12.6	NS	I	39	10	Y	3.3 ± 3.3	NS	I
		M	55.4 ± 9.8					M	29.0 ± 9.8		
		O	35.4 ± 9.8					O	25.3 ± 10.6		
19	10	Y	14.5 ± 6.7	NS	I	40	7	Y	36.7 ± 13.8	NS	I
		M	34.2 ± 12.2					M	37.1 ± 18.2		
		O	15.0 ± 10.7					O	35.7 ± 14.7		
23	9	Y	35.1 ± 10.5	a	VI	41	8	Y	76.0 ± 11.0	NS	I
		M	82.4 ± 11.1	b				M	76.3 ± 9.2		
		O	55.9 ± 10.1	ab				O	82.3 ± 9.8		
24	11	Y	54.2 ± 11.4	NS	I						
		M	65.9 ± 11.2								
		O	62.9 ± 13.3								

Table 5.4: Mean suitability of young (Y), medium aged (M), and old (O) diamondback moth eggs for Trichogrammatidae species/strains. Means followed by different letters are statistically different at $P < 0.05$ (Friedman two-way nonparametric analysis of variance by ranks)

Strain	N	Host age	% Suitability ± s.e.	Type	Strain	N	Host age	% Suitability ± s.e.	Type
2	11	Y	58.2 ± 10.8 ab		29	10	Y	36.6 ± 9.5	
		M	87.8 ± 4.1 a	VI			M	58.2 ± 8.1 NS	I
		O	30.2 ± 6.1 b				O	54.6 ± 10.7	
5	11	Y	52.4 ± 8.0		34	15	Y	57.2 ± 7.1 a	
		M	79.4 ± 8.4 NS	I			M	83.4 ± 4.2 b	VI
		O	67.3 ± 9.3				O	69.5 ± 4.4 ab	
6	17	Y	49.4 ± 6.5 a		35	13	Y	80.9 ± 3.7 a	
		M	86.6 ± 4.1 b	IX			M	88.6 ± 3.0 a	II
		O	77.9 ± 4.8 b				O	54.1 ± 7.9 b	
8	15	Y	41.4 ± 7.5 a		36	12	Y	79.2 ± 5.5	
		M	86.1 ± 6.8 b	IX			M	91.4 ± 3.2 NS	I
		O	70.2 ± 7.0 b				O	78.0 ± 6.5	
10	9	Y	67.4 ± 7.4		37	7	Y	56.7 ± 13.9 ab	
		M	82.4 ± 6.7 NS	I			M	95.8 ± 2.9 a	VI
		O	49.5 ± 14.8				O	56.5 ± 12.1 b	
14	10	Y	52.3 ± 7.7 a		38	10	Y	82.3 ± 5.0	
		M	82.8 ± 5.9 b	VI			M	91.1 ± 2.4 NS	I
		O	67.0 ± 8.3 ab				O	69.3 ± 7.6	
15	10	Y	44.7 ± 9.7		39	11	Y	79.3 ± 5.2	
		M	70.6 ± 4.9 NS	I			M	83.8 ± 4.9 NS	I
		O	44.5 ± 8.8				O	57.5 ± 6.5	
20	11	Y	83.1 ± 6.8		40	7	Y	52.3 ± 9.5	
		M	85.5 ± 4.6 NS	I			M	84.3 ± 10.2 NS	I
		O	69.6 ± 10.2				O	44.5 ± 12.7	
23	10	Y	79.2 ± 8.5		41	10	Y	73.1 ± 7.7	
		M	90.2 ± 5.6 NS	I			M	68.8 ± 9.3 NS	I
		O	60.4 ± 9.9				O	63.0 ± 9.0	
25	7	Y	81.3 ± 4.1 a						
		M	74.0 ± 6.5 a	II					
		O	30.1 ± 8.3 b						

Table 5.5: Mean clutch size allocated in young (Y), medium aged (M), and old (O) cabbage looper eggs, and for different Trichogrammatidae species/strains. Means followed by different letters are statistically different at $P < 0.05$ (Friedman two-way nonparametric analysis of variance by ranks)

Strain	N	Host age	Clutch size ± s.e.	Type	Strain	N	Host age	Clutch size ± s.e.	Type
4	10	Y	2.07 ± 0.09 a	II	23	12	Y	2.26 ± 0.13 a	II
		M	1.98 ± 0.10 ab				M	2.35 ± 0.14 a	
		O	1.39 ± 0.13 b				O	1.74 ± 0.12 b	
5	7	Y	2.62 ± 0.37	I	24	8	Y	2.10 ± 0.18	I
		M	2.14 ± 0.30 NS				M	1.88 ± 0.13 NS	
		O	1.90 ± 0.24				O	1.42 ± 0.13	
6	9	Y	2.61 ± 0.32	I	26	6	Y	2.13 ± 0.06	I
		M	2.47 ± 0.20 NS				M	2.33 ± 0.25 NS	
		O	2.20 ± 0.18				O	1.68 ± 0.17	
7	8	Y	2.40 ± 0.14 a	III	28	9	Y	2.28 ± 0.11 a	V
		M	2.00 ± 0.00 ab				M	1.39 ± 0.14 b	
		O	1.41 ± 0.15 b				O	1.53 ± 0.17 b	
8	8	Y	2.54 ± 0.23 ab	VI	31	11	Y	2.27 ± 0.19 a	III
		M	2.98 ± 0.26 a				M	1.82 ± 0.27 ab	
		O	2.21 ± 0.15 b				O	1.32 ± 0.14 b	
9	11	Y	1.75 ± 0.13 a	III	33	9	Y	2.07 ± 0.20 a	III
		M	1.34 ± 0.10 ab				M	1.84 ± 0.21 ab	
		O	1.14 ± 0.06 b				O	1.24 ± 0.05 b	
13	7	Y	2.14 ± 0.11 a	III	34	12	Y	2.33 ± 0.11 a	II
		M	2.03 ± 0.20 ab				M	2.33 ± 0.12 a	
		O	1.50 ± 0.18 b				O	1.70 ± 0.11 b	
14	10	Y	2.14 ± 0.07 a	III	36	9	Y	2.26 ± 0.28	I
		M	1.86 ± 0.19 ab				M	1.84 ± 0.15 NS	
		O	1.67 ± 0.14 b				O	1.64 ± 0.15	
15	11	Y	1.98 ± 0.14	I	37	8	Y	2.09 ± 0.19	I
		M	1.80 ± 0.10 NS				M	2.00 ± 0.09 NS	
		O	1.53 ± 0.12				O	1.77 ± 0.13	
20	11	Y	2.02 ± 0.12 a	III	38	10	Y	2.04 ± 0.14 a	III
		M	1.69 ± 0.14 ab				M	1.83 ± 0.15 ab	
		O	1.35 ± 0.09 b				O	1.53 ± 0.08 b	
21	9	Y	1.79 ± 0.17 a	II	41	8	Y	2.69 ± 0.13 a	II
		M	2.12 ± 0.13 a				M	2.59 ± 0.22 a	
		O	1.28 ± 0.08 b				O	1.34 ± 0.11 b	
22	8	Y	1.88 ± 0.11	I					
		M	1.94 ± 0.09 NS						
		O	1.35 ± 0.12						

Table 5.6: Mean clutch size allocated in young (Y), medium aged (M), and old (O) imported cabbageworm eggs, and for different Trichogrammatidae species/strains. Means followed by different letters are statistically different at $P < 0.05$ (Friedman two-way nonparametric analysis of variance by ranks)

Strain	N	Host age	Clutch size ± s.e.		Type
3	6	Y	3.00 ± 0.12		
		M	2.25 ± 0.07	NS	I
		O	2.50 ± 0.14		
23	6	Y	2.58 ± 0.07	a	
		M	2.08 ± 0.11	ab	III
		O	1.94 ± 0.02	b	
24	7	Y	3.11 ± 0.16		
		M	2.17 ± 0.08	NS	I
		O	2.29 ± 0.10		
26	6	Y	2.54 ± 0.09		
		M	1.92 ± 0.05	NS	I
		O	1.75 ± 0.07		
41	8	Y	3.14 ± 0.10		
		M	2.75 ± 0.08	NS	I
		O	2.28 ± 0.09		

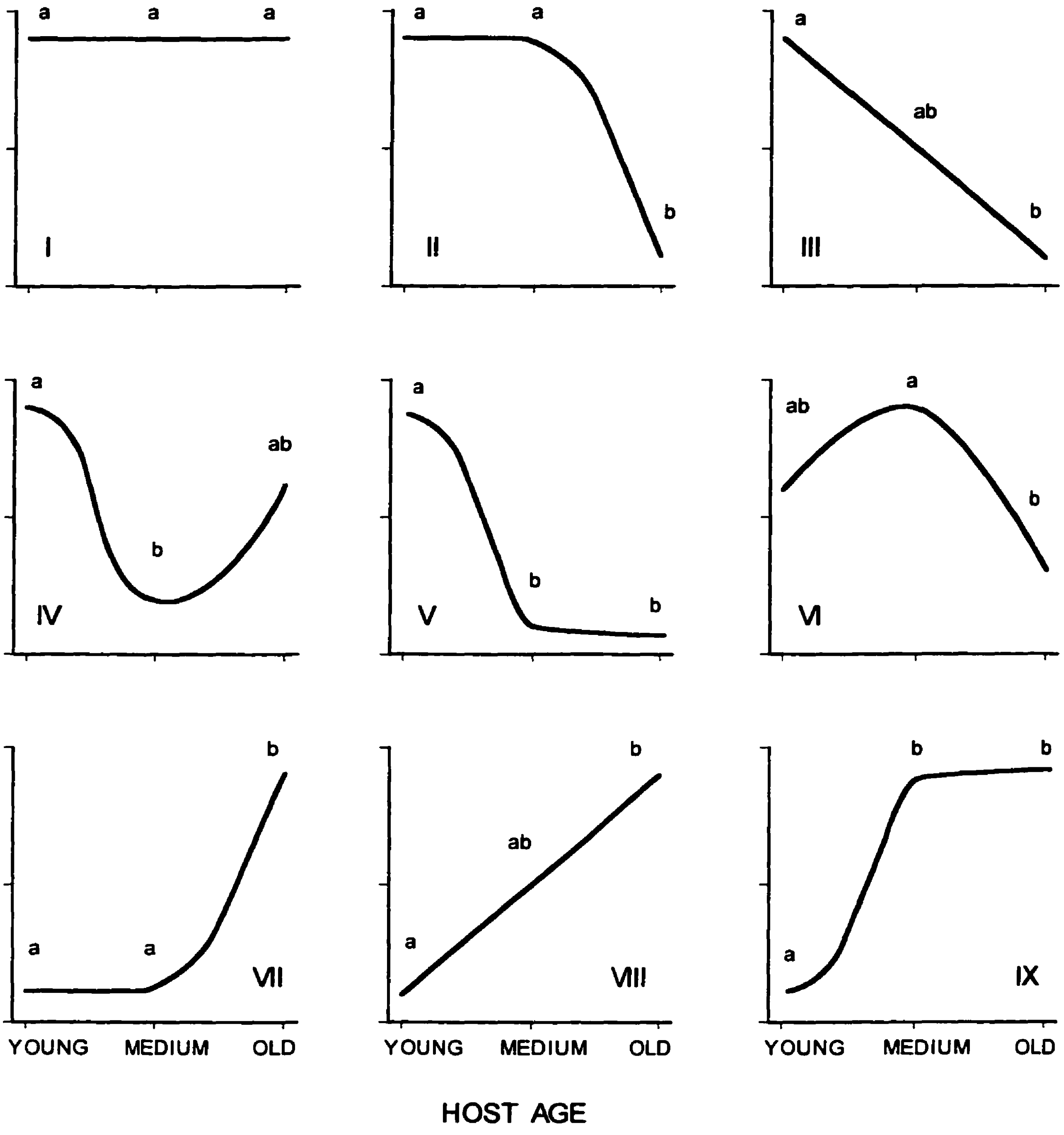


Figure 5.1: Possible types of relationship between host age and the degree of parasitism, host suitability, parasitoid progeny per host, and offspring sex ratio (modified from Pak 1986). Host age classes followed by different letters are statistically different.

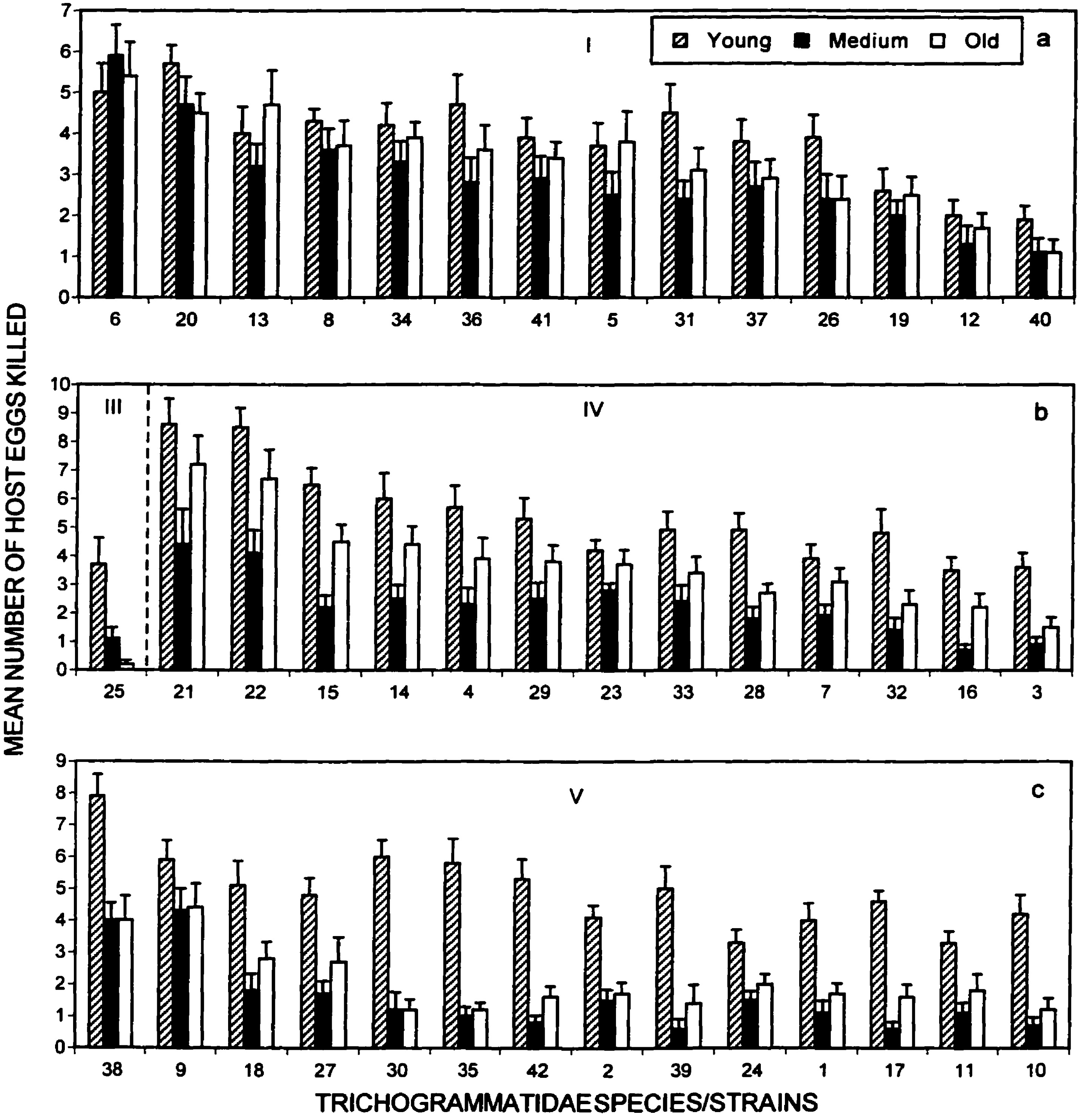


Figure 5.2: Parasitism of Trichogrammatidae species/strains according to age of cabbage looper eggs. Refer to Fig. 5.1 for relationship types classification.

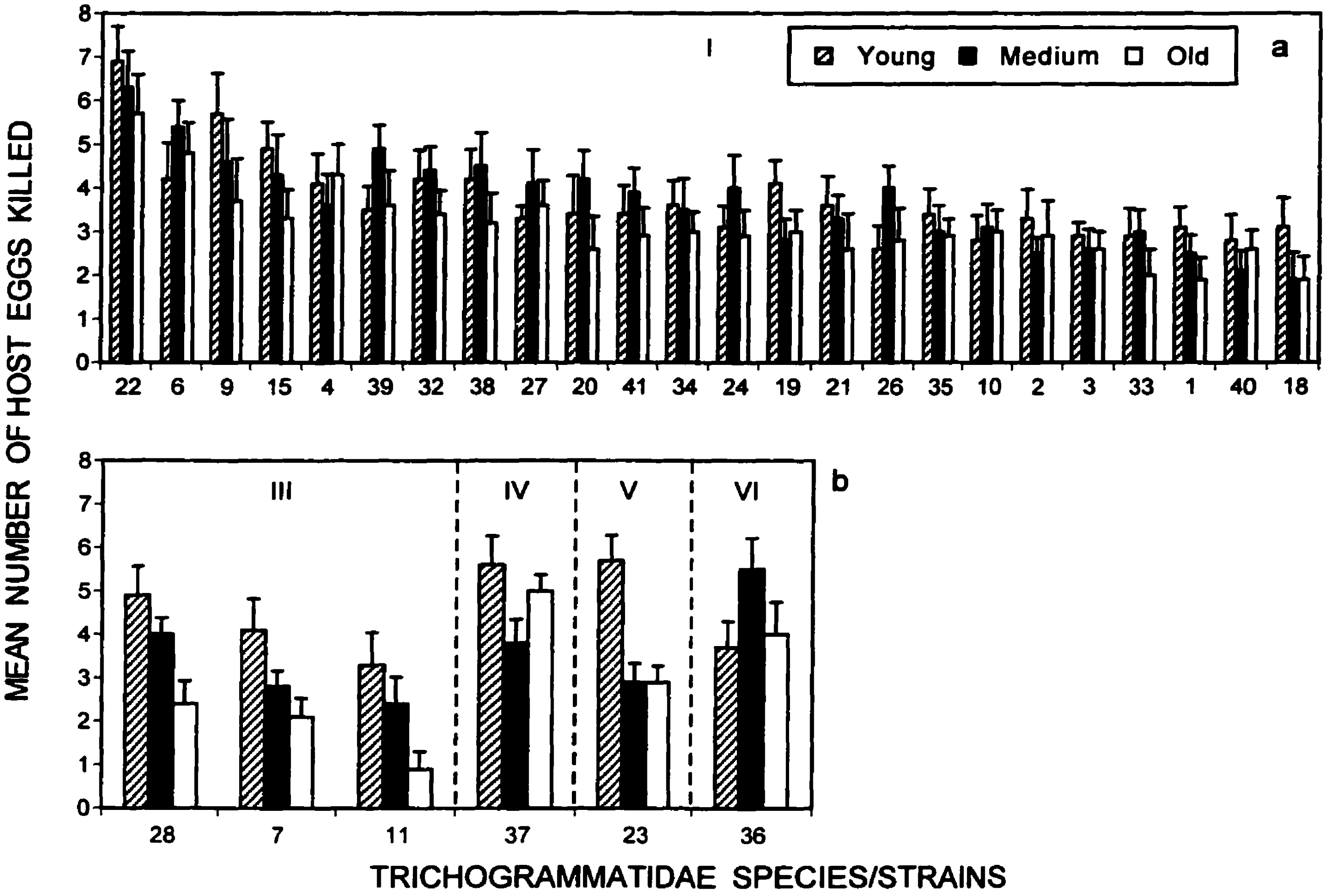


Figure 5.3: Parasitism of Trichogrammatidae species/strains according to age of imported cabbageworm eggs. Refer to Fig. 5.1 for relationship types classification.

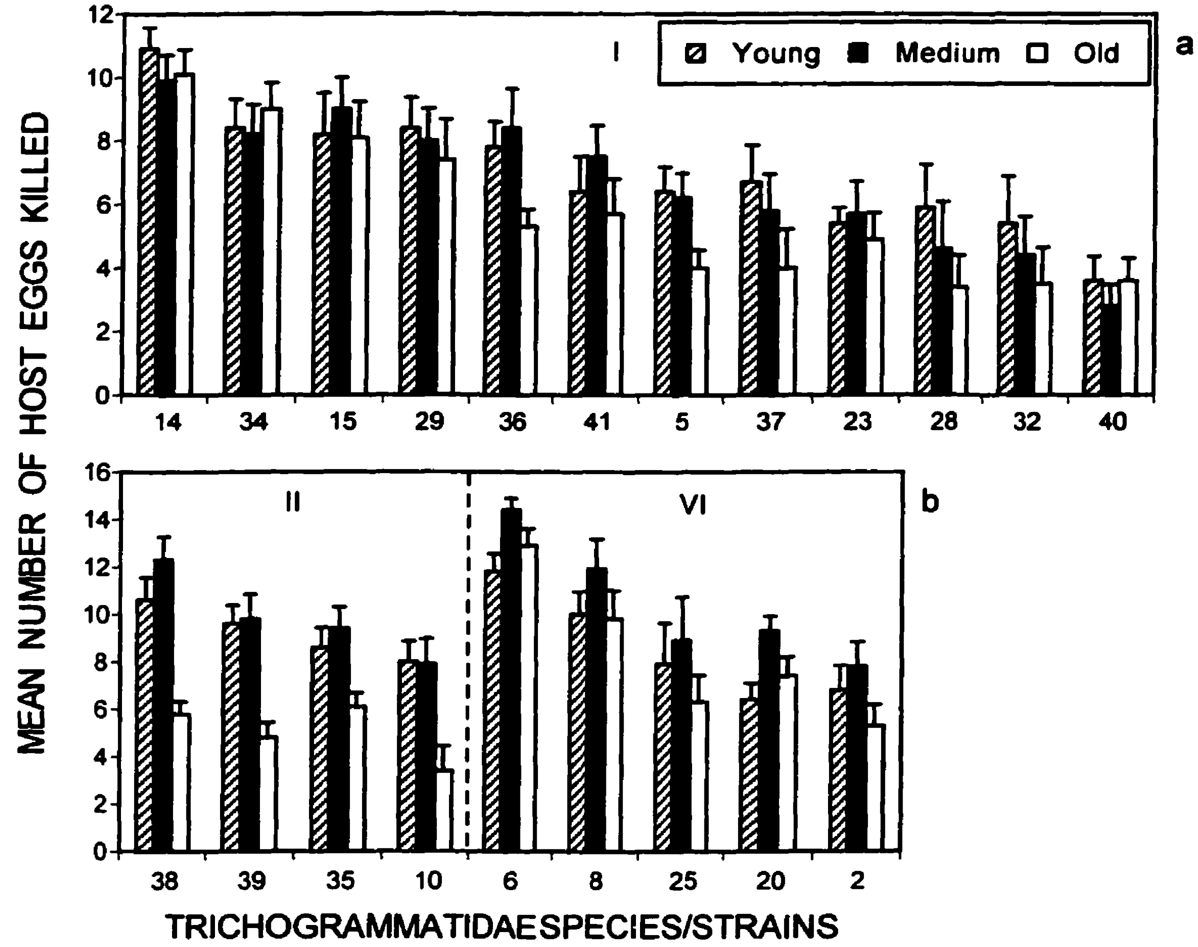


Figure 5.4: Parasitism of Trichogrammatidae species/strains according to age of diamondback moth eggs. Refer to Fig. 5.1 for relationship types classification.

VI. GENERAL CONCLUSION

The objectives of this research were (1) to estimate the seasonal occurrence of lepidopterous pests of cruciferous crops in southwestern Quebec, in order to evaluate degree-day (DD) accumulations for the prediction of generations; (2) to estimate the abundance of pest species and the composition of the parasitoid complex before introducing new parasitoids; and (3) to investigate the impact of host age on the parasitism of several egg parasitoids species (Hymenoptera: Trichogrammatidae), in order to determine the species that would be the most suitable biological control agents according to this criteria, and to understand further the behavior of egg parasitoids when their hosts vary in quality. During the two years of field study, the number and duration of generations for the most important lepidopterous species, the imported cabbageworm (ICW), the diamondback moth (DBM) and the cabbage looper (CL), were assessed on early and late plantings of cabbage and broccoli, and on Brussels sprouts.

I concluded that the DBM is a potential pest for both early and late plantings of crucifers, during its three to four generations that occur annually, and that, because of considerable overlapping between generations, weekly sampling of larvae on plants would be preferable to the use of DD accumulations in order to synchronize control treatments. Moth catches in pheromone traps could be useful to monitor temporal occurrence of the DBM, but not for the abundance of the pest on plants. Concerning the ICW, it is principally a pest during its third (and last) generation, and on late plantings. All crucifers are not affected equally, as a strong preference was found for late plantings of broccoli. DD accumulations could be used, in conjunction with plant sampling, to synchronize treatments against this species, which showed little overlapping between generations. Counts of ICW butterflies over a small area of the crops could also be used to estimate the level of infestation, but not the occurrence of the first generation. The consideration of the CL as an occasional pest was confirmed by field observations: it occurred only late in the summer, and its populations were too low and infrequent for DD analysis.

It was important to identify and quantify the impact of natural enemies of the pests, as this basic information is necessary to evaluate the impact of eventual Trichogrammatidae introductions, or other biological control agents, in this system. The parasitoid web approach was chosen to consider the *Brassica* - Lepidoptera - natural enemies system as a whole, in order to discuss the relative importance of the lepidopterous pests, their parasitoids, hyperparasitoids, and pathogens, in a pesticide free cruciferous crops system.

The analysis revealed the occurrence of up to fourteen parasitoid (12 Hymenoptera; 2 Diptera) and three hyperparasitoid species (Hymenoptera), and of seven lepidopterous species. All but one parasitoid species were specific to larval or pupal stages of their hosts, and were found attacking only one host species. Parasitoid species richness appeared to be limited by their restrictive host ranges, while hyperparasitoids were mostly limited by the abundance of parasitoid species. In addition, the regular occurrence of pathogens probably interacted with other natural enemies while increasing the mortality of lepidopterous pests. This whole dynamic system was mostly independent on the plant variety considered, as none of the crucifers studied benefited from an increased natural enemies mortality on the pests.

The parasitoid web approach is helpful in determining the qualitative and quantitative impact of a natural enemy introduction. The egg stage of the lepidoptera studied was virtually unparasitized in this area and this will facilitate the evaluation of *Trichogramma* releases in the future, and the competition with other natural egg parasitoids will likely be negligible.

This study also revealed that the most abundant pest species in southwestern Quebec, the ICW, is now parasitized to a large extent by *Cotesia rubecula* (Marshall), a species recently introduced in some areas of North America, but not in Quebec. Its establishment is further confirmed by its overwintering capabilities under laboratory conditions. With this added species, the parasitoid complex of the ICW is now similar to that in Europe, the region where the pest and its parasitoids probably came from.

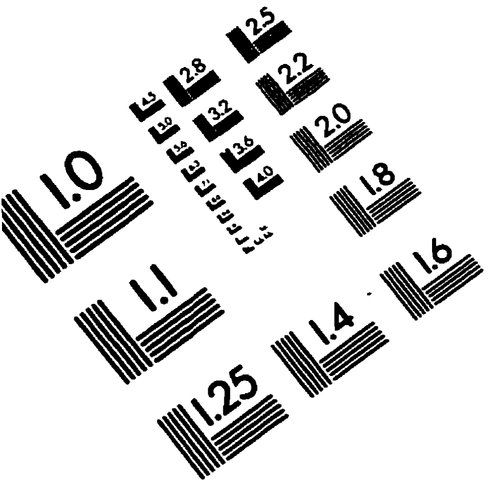
However, despite their relative importance, natural mortality factors were insufficient to maintain all lepidopterous pests at acceptable levels. This is explained by mortality occurring too late in the larval development of the pests, and too late in the season. Control measures that focus on early stages of the pests would help to prevent important damages to plants, as the pests would be killed before the larvae reached their most damaging stages.

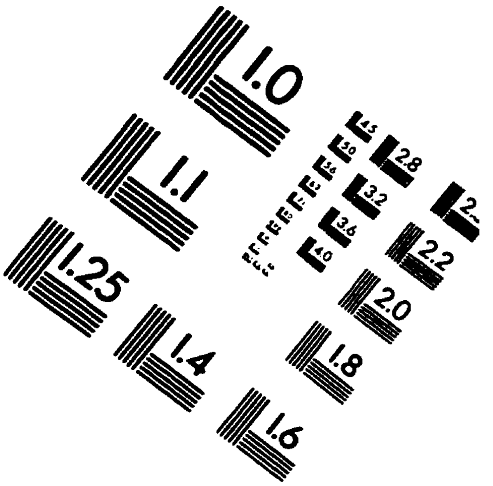
Concurrently to these field studies, laboratory experiments were carried out to evaluate egg parasitoids (Trichogrammatidae) for the biological control of the ICW, DBM, and the CL. Forty two species and strains were obtained from various parts of the world, and selection tests were carried out in order to determine the most interesting ones. The present study dealt with host age as a host quality factor influencing the parasitism rate of Trichogrammatidae.

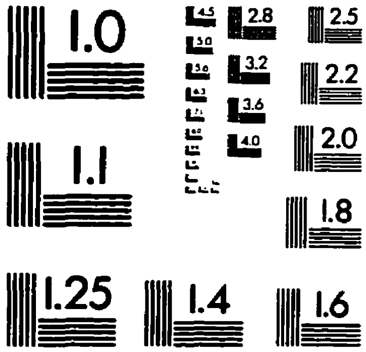
This host age investigation was the most ambitious study ever published on the subject, and it allowed for the combination of both practical and theoretical considerations. Practically, the Trichogrammatidae species that would be the more efficient in the control of the pests are those that do not discriminate between young and old host eggs. Species that show a preference for a particular host age, because of their limited host age range, will impose a supplemental time constraint for their release as compared to non-discriminating species.

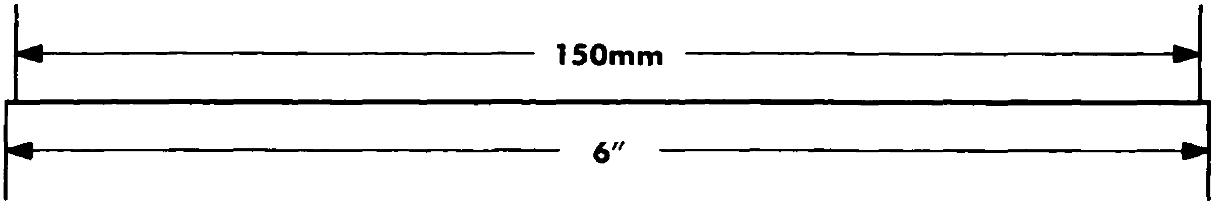
The response of egg parasitoids to host age, however, can be explained theoretically by optimal foraging strategies. When having a choice between hosts varying in quality, the progeny allocation of a female parasitoid is expected to change, as relatively high quality hosts should be the preferred hosts, with more offspring being allocated in them. Host quality factors such as host size and species have previously been investigated in relation with optimal foraging, but host age was rarely considered in that sense. This study confirms that host age is perceived by several Trichogrammatidae, and that ovipositing females respond generally by preferring young hosts, and by reducing the number of offspring when older hosts are accepted for oviposition.

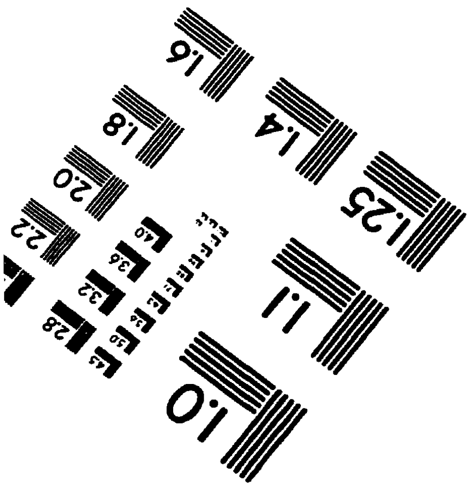
IMAGE EVALUATION
TEST TARGET (QA-3)











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